SHOUT
SHARE
IT

S. B. M.
1035

10

BM Z

GENERAL
7 OCT 1977
LIBRARY
NATURAL HISTORY

BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

ZOOLOGY

Vol. 29

1976

BRITISH MUSEUM (NATURAL HISTORY)
LONDON: 1977

DATES OF PUBLICATION OF THE PARTS

No. 1	22 January 1976
No. 2	13 April 1976
No. 3	13 April 1976
No. 4	23 April 1976
No. 5	27 May 1976
No. 6	27 May 1976

ISSN 0007-1498

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

GENERAL
7 OCT
LIBRARY

CONTENTS

ZOOLOGY VOLUME 29

PAGE
No. 1. A review of the family Centropomidae. By P. H. Greenwood . 1
No. 2. Fossil reptiles from Aldabra Atoll, Indian Ocean. By E. N. Arnold 83
No. 3. A review of the family Canidae, with a classification by numerical methods. By J. Clutton-Brock, G. B. Corbett and M. Hills . 117
No. 4. The cranial musculature and taxonomy of characoid fishes of the tribes Cynodontini and Characini. By G. J. Howes 201
No. 5. Designation of lectotypes of some ostrocods from the Challenger Expedition. By H. S. Puri and N. C. Hulings (Pls 1–27) . . 249
No. 6. Some tertiary and recent Conescharelliniform Bryozoa. By P. L. Cook and R. Lagaaij (Pls 1–8) 317

A REVIEW OF THE FAMILY CENTROPOMIDAE (PISCES, PERCIFORMES)

P. H. GREENWOOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 1
LONDON: 1976

A REVIEW OF THE FAMILY CENTROPOMIDAE (PISCES, PERCIFORMES)

BY

PETER HUMPHRY GREENWOOD

Pp. 1–81 ; 37 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 1
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 29, *No.* 1 *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Zool.)

ISSN 0007–1498

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 22 January 1976 *Price* £5.85

A REVIEW OF THE FAMILY CENTROPOMIDAE (PISCES, PERCIFORMES)

By P. H. GREENWOOD

CONTENTS

Page

INTRODUCTION 4
MATERIALS 5
ABBREVIATIONS USED IN TEXT-FIGURES 8
THE FAMILY CENTROPOMIDAE 10
AN ANATOMICAL AND TAXONOMIC REVIEW OF THE *Lates* AND *Luciolates* SPECIES 12
  The neurocranium 14
  Hyopalatine arch and the preoperculum 27
  Circumorbital bones 31
  Opercular bones 32
  Jaws 34
  Branchial skeleton 35
  Hyoid arch 38
  Pectoral girdle and associated bones 39
  Vertebral column 42
  Caudal fin skeleton 44
  Dorsal and anal fins 45
  Swimbladder 47
  Baudelot's ligament 47
  Lateral line 48
THE INTERRELATIONSHIPS OF SPECIES WITHIN THE GENUS *Lates*, AND THE TAXONOMIC STATUS OF *Luciolates* Blgr. 49
A REVIEW OF THE GENUS *Psammoperca* Richardson 51
  Introduction 51
  Osteology and anatomy of *Psammoperca waigiensis* 52
  Neurocranium 52
  Hyopalatine arch and the preoperculum 53
  Circumorbital bones 54
  Opercular series 55
  Jaws 55
  Branchial skeleton 55
  Hyoid arch skeleton 56
  Pectoral girdle and associated bones 56
  Vertebral column 58
  Caudal fin skeleton 58
  Dorsal, anal and pelvic fins 59
  Swimbladder 60
  Baudelot's ligament 60
  Lateral line 60
THE RELATIONSHIPS OF *Psammoperca* 60
THE RELATIONSHIPS OF *Centropomus* WITH THE LATINAE 62
  Neurocranium 62
  Hyopalatine arch 63
  Preoperculum 64

Operculum 64
Circumorbital bones 64
Jaws 64
Gill arches 64
Vertebrae 65
Predorsal bones 65
Dorsal fins 65
Anal pterygiophores 66
Caudal fin skeleton 66
Pectoral girdle and associated bones 66
Swimbladder 66
Baudelot's ligament 67
Lateral line 67
FOSSIL CENTROPOMIDAE 68
Lates species 69
Eolates species 70
BIOGEOGRAPHY 71
DIAGNOSES FOR THE CENTROPOMIDAE, ITS SUBFAMILIES, GENERA AND SUBGENERA 75
Centropomidae 75
Centropominae 76
Latinae 76
ACKNOWLEDGEMENTS 78
REFERENCES 78

INTRODUCTION

THE Centropomidae, a family of tropical estuarine, marine and freshwater percoid fishes, is represented in the New World, Africa and Asia by a total of at least 18 species (the number varying mainly with the taxonomic limits set for the family by different authors). Of the 18 species recognized, 9 occur in the New World, 7 – all freshwater species – occur in Africa and 2 in Asia.

Temporally the family has a good fossil record extending from the Eocene to prehistoric times. Geographically, however, the fossil record is restricted to Africa and Europe, and only one taxonomic division of the family, the closely related genera *Lates* and *Eolates*, is represented ; see Sorbini (1973) and Greenwood (1974).

It was, in fact, a new fossil centropomid from the neogene of Africa (Greenwood & Howes, 1975) that led to this revision. Our attempts to identify the new fossil soon made it clear that the African centropomids are more varied anatomically than had been realized previously. Also, it became obvious that the current taxonomic arrangement of the family does not reflect the probable phyletic relationships of its constituent taxa. Indeed, except for Fraser's (1968) analysis of the New World *Centropomus* species, no fully reasoned attempt has been made to interpret intrafamilial relationships along phyletic lines. Also, the presumed relationships of the Centropomidae with the Serranidae (Regan, 1913 ; Berg, 1947 ; Gosline, 1966 ; Greenwood, Rosen, Weitzman & Myers, 1966) appear to be based more on intuitive than on critical taxonomic reasoning, and need reappraisal.

Although it was for these reasons mainly that the present review was undertaken, I also hope that it may provide a step towards the clearing of that taxonomic rag-bag, the 'lower percoid fishes' (see Greenwood *et al.*, 1966 ; Gosline, 1966).

MATERIALS

GLAUCOSOMIDAE

Osteological material :

Glaucosoma burgeri	BMNH 1884.2.26:60	China	293 mm S.L.

CENTROPOMIDAE

Osteological material :

Lates calcarifer	BMNH 1873.1.21:2	Fitzroy R.	360 mm S.L. (skeleton)
Lates niloticus	Unregistered	No locality	(alizarin preparation)
Lates niloticus	BMNH 1971.2.8:186	No locality	(disarticulated skeleton)
Lates niloticus	Unregistered	'Red Sea'	(disarticulated skeleton)
Lates niloticus	BMNH 1864.6.29:5	'West Africa'	(skull and pectoral girdle)
Lates niloticus	Unregistered	Lake Rudolf	(alizarin preparation)
Lates niloticus	Unregistered	No locality	(alizarin preparations)
Lates niloticus	Unregistered	Lake No	(alizarin preparation)
Lates macrophthalmus	Unregistered	Lake Albert	(skeleton, 102 mm S.L.)
Lates longispinis	Unregistered	Lake Rudolf	(skull)
Lates microlepis	BMNH 1900.12.13:37	Albertville	(disarticulated skeleton)
Lates angustifrons	BMNH 1955.12.20:1722	Lake Tanganyika	(skull and pectoral girdle)
Lates mariae	BMNH 1955.12.20:1667	Lake Tanganyika	(skull and pectoral girdle)
Luciolates stappersi	BMNH 1955.12.20:1672	Lake Tanganyika	(disarticulated skeleton)
Luciolates stappersi	BMNH 1936.6.15: 1705–6	Lake Tanganyika	(skull)
Luciolates stappersi	BMNH 1971.6.23:76–8	Lake Tanganyika	(alizarin preparation)
Luciolates stappersi	BMNH 1975.4.23:2	Lake Tanganyika	(disarticulated skeleton from a fish 390 mm S.L.)
Psammoperca waigiensis	BMNH 1892.9.2:10–11	Borneo	(skull and pectoral girdle)
Psammoperca waigiensis	BMNH 1872.10.18:90	Cebu	(circumorbital series)
Centropomus undecimalis	BMNH 1883.12.16:1–2	Jamaica	(skull)
Centropomus ensiferus	BMNH 1861.12.12:13	No locality	(skeleton, disarticulated)
Centropomus pectinatus	BMNH 1894.12.1:5	Jamaica	(skull and pectoral girdle)

Dissected specimens :

Lates niloticus	BMNH 1907.12.2: 2915–6	Nile	227 mm S.L.
Lates niloticus	BMNH 1907.12.2: 2952–3	Nile	165 mm S.L.
Lates niloticus	BMNH 1931.11.20:1–2	Merowe	218 mm S.L.
Lates macrophthalmus	BMNH 1929.1.24:341–4	(Paratype)	275 mm S.L.
Lates macrophthalmus	BMNH 1975.1.18:1	Lake Albert	315 mm S.L.
Lates longispinis	BMNH 1932.6.13: 102–106	(Syntype)	250 mm S.L.
Lates angustifrons	BMNH 1906.9.8:87–88	Lake Tanganyika	300 mm S.L.
Lates mariae	BMNH 1955.12.20: 1628–29	Lake Tanganyika	220 mm S.L.
Luciolates stappersi	BMNH 1955.12.20: 1669–71	Lake Tanganyika	215 mm S.L.

Psammoperca waigiensis	BMNH 1892.9.2:10–11	Borneo	150 mm S.L.
Psammoperca waigiensis	BMNH 1872.10.13:90	Cebu	240 mm S.L.
Centropomus undecimalis	BMNH 1883.12.16:1–2	Jamaica	280 mm S.L.
Centropomus undecimalis	BMNH 1923.7.30:114	Rio de Janeiro	175 mm S.L.
Centropomus pectinatus	BMNH 1895.5.27:3–5	Mazatlan	245 mm S.L.

Specimens examined :

Lates calcarifer	BMNH 1863.2.23:29	Amoy	190 mm S L
Lates calcarifer	BMNH 1936.8.6:43	Queensland	260 mm S.L.
Lates niloticus	Major part of the entire collection		
Lates macrophthalmus	BMNH 1929.1.24: 340–344	(Paratypes)	145–283 mm S.L.
Lates longispinis	BMNH 1932.6.13: 102–106	(Syntypes)	115–270 mm S.L.
Lates angustifrons	Entire collection		
Lates mariae	Entire collection		
Lates microlepis	Entire collection		
Luciolates stappersi	Entire collection		
Luciolates stappersi	RGMARC 129887–889	(Tervuren Museum specimen)	407 mm S.L.
Psammoperca waigiensis	BMNH 1933.3.11:312	Culion, Philippines	110 mm S.L.
Psammoperca waigiensis	BMNH 1883.11.28:14	Singapore	165 mm S.L.
Psammoperca waigiensis	BMNH 1891.10.29:66	Ceylon	132 mm S.L.
Psammoperca waigiensis	BMNH 1939.1.17:11	Hong Kong	215 mm S.L.
Psammoperca waigiensis	BMNH 1888.11.6:5	Madras	175 mm S.L.
Centropomus undecimalis	BMNH 1936.1.31:8	Trinidad	290 mm S.L.
Centropomus undecimalis	BMNH 1906.6.23:82	Trinidad	180 mm S.L.
Centropomus pectinatus	BMNH 1920.12.22: 57–58	Trinidad	230 & 240 mm S.L.
Centropomus ensiferus	BMNH 1903.5.15:3–5	Panama	183–230 mm S. L.

Specimens radiographed:

Lates calcarifer	BMNH 1891.11.30:1–8
Lates niloticus	BMNH 1900.12.2: 2329–38
Lates macrophthalmus	BMNH 1929.1.24: 340–344
Lates macrophthalmus	BMNH 1929.4.16:39–41
Lates macrophthalmus	BMNH 1929.1.24: 341–344
Lates longispinis	BMNH 1932.6.13:102–6
Lates angustifrons	BMNH 1936.6.15: 1687–97
Lates angustifrons	BMNH 1906.9.8:87–88
Lates mariae	BMNH 1955.12.20:1636; 1628–9; 1655–6 ; 1672–86
Lates mariae	BMNH 1906.9.6:7
Lates microlepis	BMNH 1906.9.8:89
Lates microlepis	BMNH 1955.12.20: 1753–85
Luciolates stappersi	BMNH 1955.12.20: 1669–71 ; 1680

Luciolates stappersi	BMNH 1936.6.15: 1705–6
Luciolates stappersi	BMNH 1971.6.23:76–78
Psammoperca waigiensis	BMNH 1872.10.18:90
Psammoperca waigiensis	BMNH 1939.1.17:11
Psammoperca waigiensis	BMNH 1892.9.2:10–11
Psammoperca waigiensis	BMNH 1870.12.27:17
Psammoperca waigiensis	BMNH 1888.11.6:5
Centropomus unionensis	BMNH 1903.5.15:8
Centropomus robalito	BMNH 1895.5.27:6
Centropomus nigrescens	BMNH 1883.7.28:14
Centropomus ensiferus	BMNH 1903.5.15:3–5
Centropomus undecimalis	BMNH 1895.5.27:2
Centropomus undecimalis	BMNH 1936.1.31:8
Centropomus undecimalis	BMNH 1924.2.29:16

Fossil material :

Eolates gracilis	BMNH P23803	Monte Bolca	130 mm S.L.
Eolates gracilis	BMNH P16137	Monte Bolca	121 mm S.L.
Eolates gracilis	BMNH P3918	Monte Bolca	139 mm S.L.
Eolates gracilis	BMNH P23798	Monte Bolca	*c.* 135 mm S.L.
Eolates gracilis	BMNH P16374	Monte Bolca	41 mm S.L.
Eolates gracilis	BMNH P16756	Monte Bolca	29 mm S.L.
Eolates gracilis	BMNH P37225	Monte Bolca	124 mm S.L.

SERRANIDAE

Osteological material :

Epinephelus tauvina	Unregistered	Java	(skeleton, 225 mm S.L.)
Epinephelus areolatus	BMNH 1888.12.29:24	Muscat	(skeleton, 280 mm S.L.)
Epinephelus afer	Unregistered	St Croix	(skeleton, 140 mm S.L.)
Epinephelus itajara	BMNH 1883.12.16:9	Jamaica	(skeleton, 355 mm S.L.)

Dissected specimens :

Epinephalus alexandrinus	BMNH 1964.7.14:1	Malta	243 mm S.L.

Specimens examined :

Serranus radialis	BMNH 1923.7.30:77–79	Rio de Janeiro	115–140 mm S.L.

AMBASSIDAE

Osteological material :

Ambassis urotaenia	BMNH 1928.1.17:8–15	(alizarin preparation)
Ambassis commersonii	BMNH 1855.9.19:359	(disarticulated skeleton)
Ambassis wolffii	BMNH 1898.4.2:67	(skeleton, 85 mm S.L.)

Specimens examined:
The major part of the collections of *Ambassis* and *Chanda*

GERREIDAE

Osteological material :

Gerres oyena	BMNH 1965.4.4:125–38	(alizarin preparations)
Gerres oyena	BMNH 1960.3.15:670–5	(alizarin preparations)

ABBREVIATIONS USED IN THE TEXT-FIGURES

AA	Anguloarticular
ART P	Articular process of the premaxilla
ASC P	Ascending process of the premaxilla
AHYF	Anterior facet for hyomandibula
Bb 1–3	Basibranchial
'BcF'	'Berycoid foramen'
BOC	Basioccipital
BrR	Branchiostegal ray
BSP	Basisphenoid
Cb 1–5	Ceratobranchial of first to fifth arch
Ch	Ceratohyal
CL	Cleithrum
COR	Coracoid
D	Dentary
Dhh	Upper hypohyal
D PROC	Dorsal process of the maxilla
E	Mesethmoid
E1–E4	Epibranchials of the first to fourth arches
E2TP, E3TP	Tooth-plates associated with the second and third epibranchials
ECT	Ectopterygoid
Eh	Epihyal
ENT	Entopterygoid
EP	Epural
EPI	Epioccipital (= epiotic *auct.*)
EXO	Exoccipital
FR	Frontal
FRC	Frontal crest
FRR	Frontal ridge
GF	Gill filament
Gh	Glossohyal
Gr	Gill raker
H_1, H_5	First and fifth hypurals
Hb1	Hypobranchial of first gill arch
$HsPU_2$	Haemal spine of second preural vertebra
HY	Hyomandibula
IC	Intercalar
IOP	Interoperculum
LAC	Lachrymal (first circumorbital bone)
LATE	Lateral ethmoid
LAT SP	Latero-sensory canal openings
LC	Lateral commissure
LIG	Ligament
MET	Metapterygoid
$NaPU_2$	Neural arch and spine of second preural vertebra
OCS	Occipito-spinal nerve foramen
OP	Operculum
PAL	Palatine
PAR	Parietal
PARC	Parietal crest
Pb1–Pb4	Pharyngobranchials of the first to fourth gill arches
Pb2 TP–Pb4 TP	Tooth plates associated with pharyngobranchials of the second to fourth gill arches
PC_1, PC_2	Upper and lower postcleithra
PFr	Pectoral fin ray
PH	Parhypural
PHYF	Posterior facet for hyomandibula
PMAXP	Posterior maxillary process
PMXP	Premaxillary process of the maxilla
POP	Preoperculum
PRO	Prootic
PS	Parasphenoid
PTF	Posttemporal fossa
PTO	Pterotic
PTS	Pterosphenoid
PTSP	Pterosphenoid pedicle
PTSS	Pterosphenoid spur
PU_1+U_1	Fused first ural and preural centra
Q	Quadrate
R	Radial for pectoral ray
RA	Retroarticular
SC	Supracleithrum
Sc	Scapula
SLP	Supralamellar tooth plate
SOC	Supraoccipital
SOC S	Supraoccipital shelf
SOP	Suboperculum
SOS	Subocular shelf
SPO	Autosphenotic
SY	Symplectic
TP	Tooth plate
UR	Uroneural
UR1, UR2	Upper and lower uroneurals
V	Vomer
VHh	Lower hypohyal
II–V	Second to fifth circumorbital bones
IX	Foramen for glossopharyngeal nerve
X	Foramen for vagus nerve
1st APTY	First anal pterygiophore
2nd Asp	Second anal fin spine

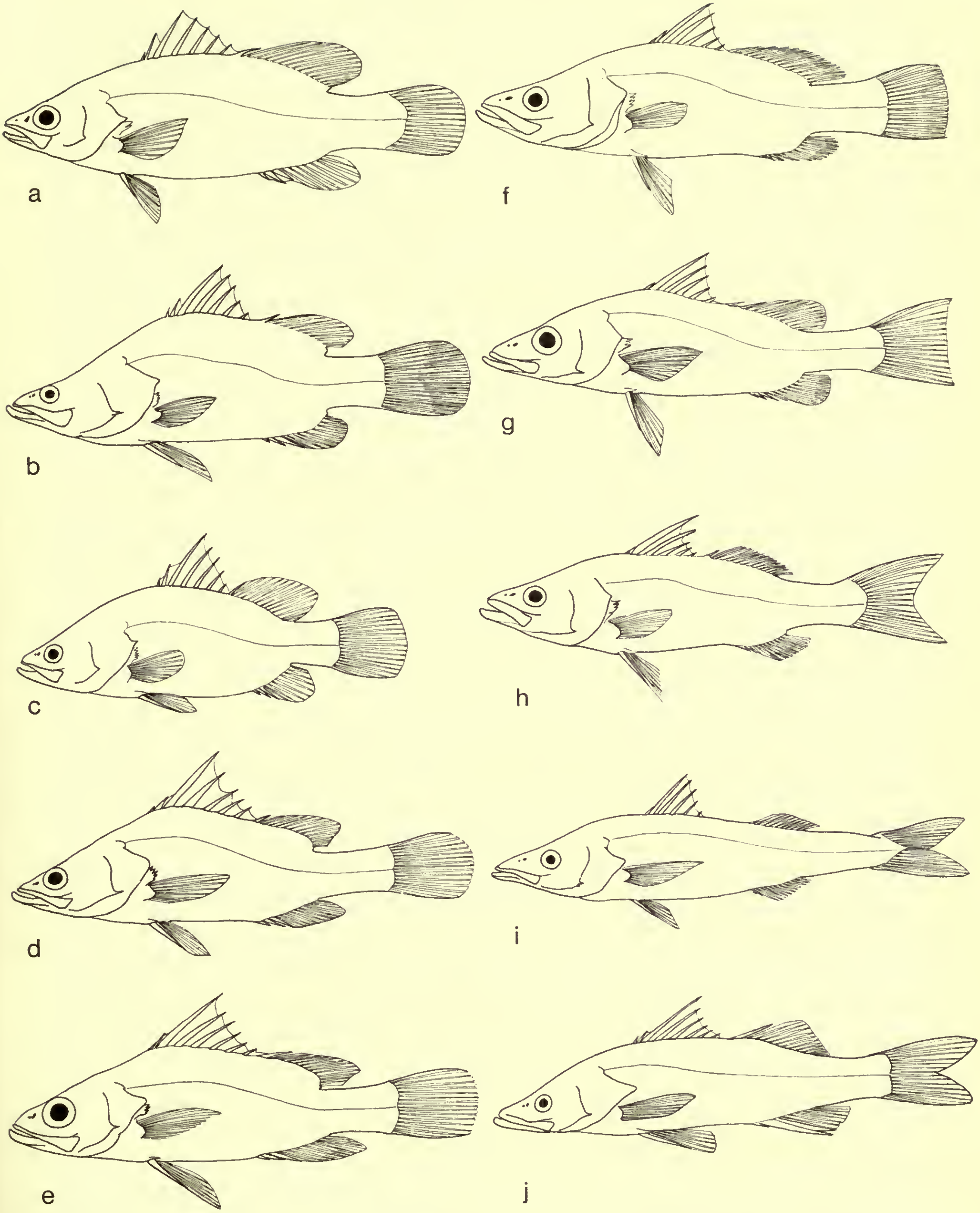


FIG. 1. Outlines of: (a) *Psammoperca waigiensis*, (b) *Lates calcarifer*, (c) *L. niloticus*, (d) *L. longispinis*, (e) *L. macrophthalmus*, (f) *L. angustifrons*, (g) *L. mariae*, (h) *L. microlepis*, (i) *L. stappersi*, (j) *Centropomus undecimalis*.

THE FAMILY CENTROPOMIDAE

Although in 1955 Matsubara classified several of the genera considered below in the family Serranidae, there is still a consensus of opinion among ichthyologists that these fishes constitute a natural taxonomic group, albeit one closely related to the Serranidae. (See Katayama (1956) for a short taxonomic history of the group.)

There has, however, been rather less agreement on the definition and delimitation of the family Centropomidae in which these various genera are classified, or with which they are thought to be most closely related. In particular there is uncertainty about the affinities of *Glaucosoma* Temm. & Schl., of *Chanda* Ham. Buch. (= *Ambassis* of authors), and of genera related to *Chanda*. Regan (1913), for example, included both *Glaucosoma* and *Chanda* (as *Ambassis*) in the Centropomidae, as did Norman (1966) who, however, gave *Chanda* and related genera subfamilial rank (Chandinae) and placed *Glaucosoma* with *Lates* Cuv., and *Psammoperca* Richardson in the subfamily Latinae. Other views were expressed by Jordan (1923) who gave familial rank both to *Chanda* and its related taxa (Ambassidae), and to *Glaucosoma* (Glaucosomidae). Berg's (1947) classification returned *Chanda* to the Centropomidae, but kept *Glaucosoma* as a monotypic family. Greenwood *et al.* (1966) followed Berg, as did Lindberg (1971).

There have, of course, been several definitions of the Centropomidae, both *sensu latu* and *stricto* (see especially Gill, 1883, and Meek & Hildebrand, 1925, for the family as restricted to species of *Centropomus* ; Regan, 1913, and Norman, 1966, for the family *sensu latu* ; Munroe, 1961, for the Chandidae and Centropomidae, and Katayama, 1954, for the only comprehensive definition of the Glaucosomidae). Yet, from none of these definitions is it possible to determine the synapomorph features that could establish the phyletic relationships of the taxa involved, either as a holophyletic assemblage or as two or even three lineages.

With the aim of establishing such relationships I have examined all the characters listed in these various definitions ; as is inevitable in such revisionary work I have discovered other characters which were not taken into account by earlier authors. Most of the characters used by Regan (1913), Norman (1966) and Katayama (1954) are either primitive features widely distributed amongst the lower percomorphs and percoids (i.e. symplesiomorphies), or, if derived ones, are characteristics also shared with several percoid families. In the symplesiomorphic category are the vertebral number, presence of frontoparietal crests, and the dentition and other jaw characters. The derived characters include the presence of an axillary pelvic scale, and the extension of lateral line pore scales onto the caudal fin. This latter character is of interest because, although the lateral line extends some way onto the caudal in several percoid taxa, rarely does it reach or almost reach to the margin of that fin, as it does in *Centropomus*, *Lates* and *Psammoperca*. (Only in the Sciaenidae does the lateral line extend as far posteriorly as in these genera.) This distinction in the degree to which the lateral line extends posteriorly has not been drawn by other workers.

One character not used by previous authors (but mentioned with reference to *Centropomus* and *Lates* by Gosline, 1966) is the presence of an anteroposteriorly expanded neural spine on the second vertebra. Indeed, this feature, combined with the extension of the lateral line far onto the caudal fin, provide the only synapomorph characters at all widely distributed amongst taxa currently classified with the Centropomidae. Because the caudal lateral line character also occurs in the Sciaenidae, the neural spine character is the sole truly synapomorph feature of the centropomids. Currently recognized genera with such an expanded neural spine are *Lates*, *Luciolates*, *Psammoperca* and *Centropomus* (Fig. 1). Except for *Luciolates*, these genera also have the caudal lateral line scale row extending or almost extending to the fin margin. (The lateral line in *Luciolates* is discussed on p. 48.)

Neither *Glaucosoma* nor *Chanda* (and its related genera) has either of these features. The lateral line extends only onto the basal third, or less, of the caudal fin, and the second neural spine is no wider than that of the first vertebra (in other words, the usual percomorph condition).

Thus, on the basis of these characters, and the lack of any other unifying features, it would seem that *Glaucosoma* and *Chanda* cannot belong to the same lineage as *Centropomus*, *Lates*, *Luciolates* and *Psammoperca*. These latter taxa alone are therefore retained in the family Centropomidae.

Questions now arise as to the relationships and status of *Glaucosoma* and the *Chanda*-like genera, of their relationship to the Centropomidae as here defined, and of the interrelationships of the Centropomidae within the Percoidei.

Nothing I have yet discovered suggests that *Glaucosoma* is a close relative of *Chanda* (and its immediate relatives). Both taxa are readily defined by various autapomorphies, but I cannot find any synapomorph characters uniting them. Unfortunately, the sort of detailed information needed for phyletic studies amongst percoid fishes is not yet available for many taxa, and I cannot suggest where the relationships of *Chanda* and *Glaucosoma* may lie. For the moment the only course available is to recognize two families, the Glaucosomidae and the Chandidae, and to consider both as of uncertain affinity amongst the Percoidei. The dorsal gill arch skeleton in the Chandidae I have examined (several species of *Chanda*) is certainly more derived than are those of the Centropomidae and Serranidae (see Rosen, 1973, for a discussion of the gill arches in percoid fishes). In the morphology of the pharyngobranchials, especially the second, *Chanda* is very similar to *Eucinostomus argenteus* (Gerridae) as figured by Rosen (op. cit., text-figs 98 & 99). *Glaucosoma* also shows more derived characters in its gill arch skeleton than does any member of the Centropomidae. I suspect that it will be from the gill arch skeleton that the relationships of these two families will ultimately be determined.

Similar problems and lack of data limit the formulation of hypotheses regarding the phylogeny of the Centropomidae. It is generally thought, or implied, that the centropomids are closely related to the Serrandiae (see Regan, 1913; Katayama, 1954; Gosline, 1966; Greenwood *et al.*, 1966; Norman, 1966). Again it has so far proved impossible to demonstrate within these families any but symplesiomorph or autapomorph features, none of which provides acceptable information for confirming or refuting this relationship. Thus, for the time being the Centropomidae too must remain as a family *incertae sedis* amongst the lower percoids.

However, with the limits of the Centropomidae defined (see above) it is now possible to turn to problems of infrafamilial relationship and taxonomy.

AN ANATOMICAL AND TAXONOMIC REVIEW OF THE *LATES* AND *LUCIOLATES* SPECIES

The present taxonomic status of several *Lates* species must be reviewed before considering their anatomy and phyletic relationships. The probably monotypic genus *Luciolates* Blgr. is also included in this review, although a discussion of its ultimate status is deferred until p. 49.

With one exception, namely *Lates calcarifer* (Bloch), all extant *Lates* species are confined to Africa but fossil remains of this genus are known from southern Europe as well as from several areas in Africa (Sorbini, 1973; Greenwood, 1974). The extinct taxon *Eolates gracilis* (Agassiz) from Monte Bolca will be considered later (p. 70), together with the extinct 'species' of *Lates*.

Lates calcarifer, a coastal and estuarine species, is widely distributed in the Indo-Pacific region (India, Bangladesh, Burma, Malay Peninsula, Java, Sumatra, Borneo, Celebes, Sarawak, Philippines, Papua–New Guinea, northern and western Australia, southern China, and Japan). According to Weber & de Beaufort (1929), this species also occurs in the Persian Gulf; their reference to *L. calcarifer* entering the mouths of the Nile, Niger and Senegal, and ascending these rivers, is clearly an error stemming from a confusion of this species with *L. niloticus*. Although essentially a marine fish, *L. calcarifer* freely enters and remains in rivers but always returns to estuarine or marine environments for spawning (Dunstan, 1959; Lake, 1971).

Lates niloticus (L.) is widely distributed in the rivers and lakes of tropical Africa (Nile, Niger, Senegal, Volta and Zaire [= Congo] rivers; Lakes Chad, Albert, Rudolf and some of the Ethiopian lakes). Not surprisingly in such a widespread taxon there are indications of some geographically limited morphotypes. As yet there has been insufficient study of these populations to determine the significance of their morphological differences, and none of the fluviatile populations has been given the formal status of a subspecies (see Daget (1954) on Pellegrin's (1922) *L. niloticus* var. *macrolepidotus* from Zaire). Worthington (1932), however, has described two subspecies, *L. niloticus rudolfianus* and *L. n. longispinis* from Lake Rudolf.

Lates niloticus rudolfianus, a form attaining a large size (up to 148 cm total length) and apparently confined to inshore regions of Lake Rudolf (Worthington, 1932), is acknowledged by Worthington to be morphologically intermediate between *L. niloticus* of the Nile and populations of that species inhabiting Lake Albert (named *L. albertianus* by Worthington [1929], but shown by Holden [1967] to be indistinguishable from *L. niloticus*). I have re-examined the type material of *L. n. rudolfianus* and can find no reason for maintaining the subspecific status of this population. In all morphometric, meristic and gross morphological characters the type specimens lie within the range of variability determined for *L. niloticus* over its entire range. Thus, at least until larger samples are available from numerous localities in Lake Rudolf, I would consider *L. niloticus rudolfianus* to be a synonym of the nominate species.

The second subspecies from Lake Rudolf, *L. n. longispinis*, presents a somewhat different problem. Apparently it is separated ecologically from the other *Lates* species in the lake, being a fish of the deeper waters (Worthington, 1929; Hopson, unpublished report). Furthermore, it is morphologically differentiable from *L. niloticus*, and does not attain such a large adult size.

The principal morphometric differences distinguishing the taxon '*longispinis*' from *L. niloticus* are its larger eye (diameter 22·6–39·9 per cent of head in fishes 118–273 mm standard length, cf. 18·3–22·9 per cent in *L. niloticus* of a comparable size; in both taxa eye size is negatively correlated with standard length) and longer third spine in the dorsal fin (78·0–84·0 per cent of head, cf. 55·0–70·0 per cent). The larger eye in '*longispinis*' is most clearly manifest when small specimens of both species are compared; for example the eye is 21·8 per cent of the head in a 107 mm S.L. *L. niloticus* but is 32·9 per cent in a 118 mm specimen of '*longispinis*'.

Another difference, but one correlated with relative eye size, lies in the less marked posterior extension of the maxilla in '*longispinis*'. In specimens of *L. niloticus* more than 125 mm S.L. the posterior tip of the maxilla lies at a point clearly behind a vertical through the posterior orbital margin; in '*longispinis*' above 125 mm long the maxillary tip lies in or a little anterior to that vertical. In fishes less than 120 mm S.L., the distinction is much less obvious (or even non-existent) because of the relatively larger eye in *L. niloticus* of that size.

Since, in Lake Rudolf, '*longispinis*' and *L. niloticus* are sympatric (albeit allotopic), and because the two taxa show various and consistent morphological differences, I can find no grounds for considering '*longispinis*' to be a subspecies of *L. niloticus*. The obvious expedient of raising Worthington's (1932) *L. n. longispinis* to full specific rank, however, requires further consideration when the taxon is compared with *L. macrophthalmus* Worthington, 1929 (see above; also Holden, 1967). *Lates macrophthalmus* is the endemic ecological counterpart in Lake Albert of '*longispinis*' in Lake Rudolf (see Holden, 1967), and closely resembles that species as well, sharing with it the presumably derived features of enlarged eyes and elongate third spine in the dorsal fin. The only differential feature I can find is the relatively longer spine of '*longispinis*' (78·0–85·0, mean 82·0 per cent of head, cf. 65·0–84·0, m = 74·4 per cent, in *L. macrophthalmus*). There also appear to be slight differences in the relative proportions of certain head parts, e.g. the vertical limb of the preoperculum lies slightly further forward in '*longispinis*'. Detailed comparisons are hampered by the paucity of study material, there being only the five syntypes of *L. n. longispinis** and the eleven syntypes of *L. macrophthalmus* available.

Basically, the problem raised by '*longispinis*' in Lake Rudolf and *L. macrophthalmus* in Lake Albert is whether each should be considered a distinct and endemic species evolved locally from a population of *L. niloticus* (the generally accepted hypothesis, see Worthington, 1932, and Holden, 1967) or whether they should be looked upon as sister taxa derived from a common ancestor distinct from *L. niloticus*. This hypothetical species presumably invaded the developing Lakes Rudolf and Albert alongside *L. niloticus*. If this latter relationship could be determined it would, on the morphological evidence available, be more realistic to treat '*longispinis*' as a subspecies of *L. macrophthalmus* rather than as a distinct species. Unfortunately I do not have enough material at my disposal to test the two hypotheses, even assuming that anatomical criteria alone would be suitable for this purpose. For the moment then, and without prejudice to an ultimate solution of the taxon's true phyletic position, I propose treating Worthington's subspecies as a full species, namely *L. longispinis* Worthington (1932).

---

* The sixth syntype of *L. n. longispinis* mentioned by Worthington (1932) cannot be located, and neither is it recorded in the Museum's register. This suggests that the word 'six' in the original description is a *lapsus* for 'five'.

The three other *Lates* species, *L. angustifrons* Blgr., *L. microlepis* Blgr. and *L. mariae* Steindachner (see Poll, 1953), require no further comment at this stage. All are morphologically distinct from the other species and from one another.

A fourth *Lates*-like taxon from Lake Tanganyika is currently placed in the genus *Luciolates** Blgr., principally because of the wide separation of the two dorsal fins (Boulenger, 1914; Poll, 1953, 1957). *Luciolates* is closely related to *Lates*, in particular to *L. mariae*. As I hope to demonstrate in the next section of this paper I believe that *Luciolates* should be included in *Lates* if the principles of phyletic classification are not to be violated.

The anatomy of *Lates* and *Luciolates*

The anatomy, and especially the osteology, of *Lates* and *Luciolates* has never been subject to a general review encompassing all known species. Gregory (1933) has given a rather superficial account of the syncranial osteology in *Lates niloticus*,† and Katayama (1956) a more detailed description of *Lates calcarifer* which included some details of its soft anatomy.

The account which follows is based on the examination of at least two skeletons of each species, and in the case of *L. niloticus* on several specimens over a wide size range. Radiographs of several specimens of every species were also examined.

In all intrageneric comparisons made below the conditions found in *L. calcarifer* and *L. niloticus* are, with few exceptions, taken to be those primitive for the genus. This conclusion regarding the status of the two species was reached after all the species had been examined and a comparison made with members of other percoid groups apparently related to the Centropomidae (Gosline, 1966; Greenwood *et al.*, 1966). Within the Centropomidae as a whole, *L. calcarifer* and *L. niloticus*-type cranial osteology should also be taken to represent the primitive condition.

The neurocranium

The overall morphology of the neurocranium in *Lates* and *Luciolates* can be judged from Figs 2–8.

Basically, the neurocranium in *Lates* differs little from that of most serranids (*sensu* Greenwood *et al.*, 1966). It has, however, well-developed and continuous frontoparietal crests with a sensory canal pore located at or near the junction of the crests, and the exoccipital facets are contiguous (separated in most serranids,

---

* A second species, *Luciolates brevior*, has been described (Boulenger, 1914), but is known only from the holotype and has never been recorded again. In all probability *L. brevior* should be treated as a synonym of *Luciolates stappersi* Blgr., 1914, and is treated as such in this paper.

† The neurocranium supposedly of *Luciolates stappersi*, figured by Gregory (1933), is wrongly identified; as far as I can judge it is from a specimen of *Lates angustifrons*.

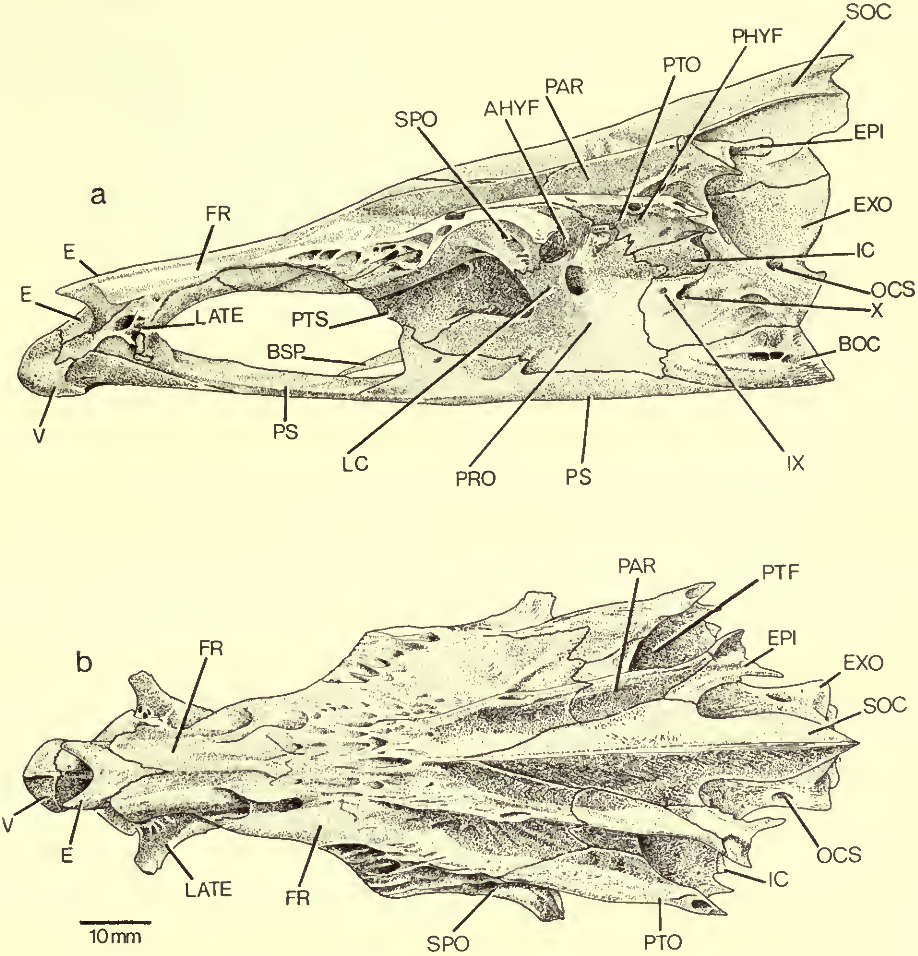

a
SOC
PHYF
PTO
PAR
AHYF
SPO
EPI
EXO
FR
E
E
LATE
PTS
BSP
IC
OCS
X
BOC
V
PS
LC
PRO
PS
IX
b
PAR
PTF
EPI
EXO
SOC
FR
V
E
LATE
FR
OCS
IC
10mm
SPO
PTO

FIG. 2. *Lates niloticus*, neurocranium. (a) Left lateral view. (b) Dorsal view. (From Greenwood & Howes, 1975.)

personal observations; see also Gosline, 1966). Since continuous frontoparietal crests (usually incorporating a sensory pore) occur in berycoid fishes (see Patterson, 1964), this condition must be considered a primitive one. Likewise, the medially contiguous exoccipital facets are also a primitive feature found in berycoids. The extensive interfrontal penetration of the supraoccipital, however, must be ranked as a derived feature.

The dorsicranium shows some slight interspecific differences in detail but not in basic layout. The supraoccipital extends forward to the level of the median sensory pore of the supraorbital lateral line cross-commissure, and clearly separates the frontals posteriorly. The bone's relative anterior extension appears to be least marked in *L. angustifrons*, *L. mariae* and *L. microlepis*; this is attributable to the

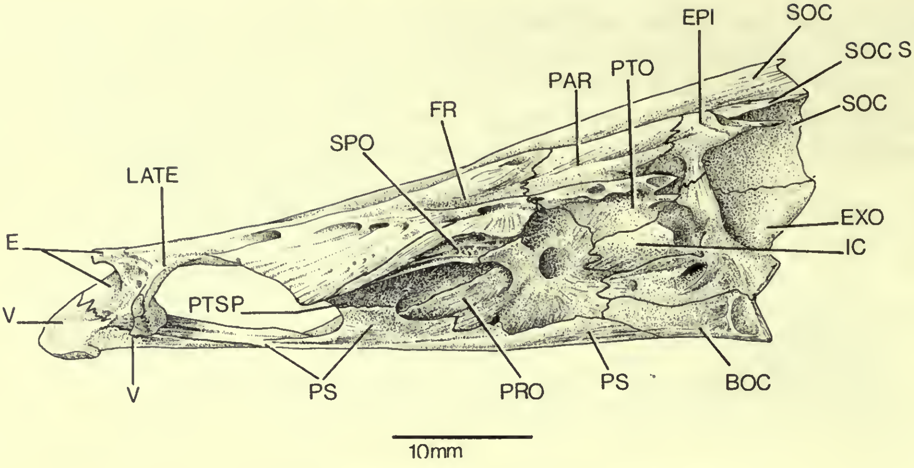


FIG. 3. *Lates calcarifer*, neurocranium, left lateral view.

anteriorly more elongate frontals, a lengthening associated with the elongation of the ethmoid region in these species. In *Luciolates stappersi*, despite the attenuation of its snout, the supraoccipital extends forward to a point level with the anterior orbital margin ; the median sensory pore has a corresponding anterior displacement (Fig. 8).

These four Lake Tanganyika species also have deeper grooves lying between the median supraoccipital crest and the fronto-parietal ridges on each side of the skull, a consequence, perhaps, of their narrower skulls (see below).

All *Lates* species have a well-demarcated ledge on either side of the supraoccipital crest, the ledge being confluent anteriorly with the supraocciptal bone itself, and extending backwards almost to the posterior margin of the crest. The ledge is narrower and less conspicuous in *Luciolates*, and is confined to the anterior part of the crest.

The posttemporal fossa is deep in all species except *Luciolates stappersi*, and in none do its constituent bones meet at the centre of the fossa ; even in the largest specimen examined the fossa is still open, its aperture closed off from the cranial cavity by a tough membrane. Amongst members of the Serranidae the *Lates*–*Luciolates* condition is characteristic of small and apparently juvenile fishes ; in larger individuals (many of which are, nevertheless, considerably smaller than adult *Lates*) the fossa has a completely bony floor. This interfamilial difference would suggest that the *Lates* condition is the primitive one.

The wide cephalic lateral line canals of the dorsicranium are completely bone enclosed in all species (including *Luciolates*). On each side of the skull the continuous supraorbital–temporal canal opens to the exterior through several pores.

Dorsal and lateral skull outlines are essentially similar in *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis* except for a marked narrowing of the interorbital region in the two latter species, and a more forward position of the orbit in *L. calcarifer*. The ethmoid region is relatively short, and the parasphenoid runs forward in the same line as the base of the braincase. The preotic skull proportions of the largest *L. niloticus* examined (neurocranial length 228 mm) are very similar to those in a much smaller *L. calcarifer* skull (103 mm long, from a fish of *c.* 40 cm S.L.), and differ from those in smaller *L. niloticus* skulls. The most noticeable differences apparent when these smaller *L. niloticus* skulls are compared with the skull of an equal-sized *L. calcarifer* are the relatively more anterior position of the orbit, and the much longer precommissural skull region in the latter species (see below, p. 20). The skull proportions of large *L. niloticus* (i.e. skulls > 150 mm long), however,

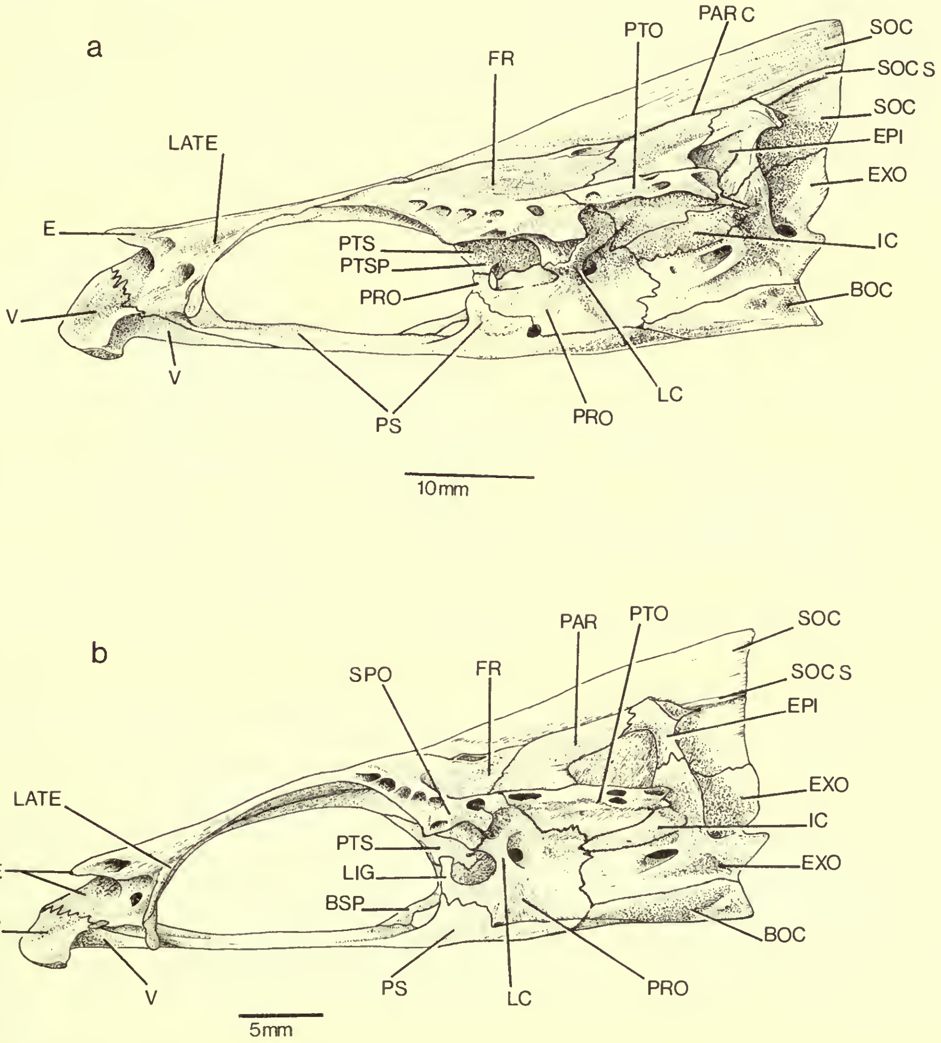

a
PAR C
PTO
SOC
FR
SOC S
SOC
EPI
LATE
EXO
E
PTS
IC
PTSP
PRO
BOC
V
V
LC
PS
PRO
10mm
b
PAR
PTO
SOC
SPO
FR
SOC S
EPI
EXO
LATE
IC
PTS
E
LIG
EXO
BSP
V
BOC
PS
LC
PRO
V
5mm

FIG. 4. (a) *Lates longispinis*. (b) *L. macrophthalmus*. Neurocranium in left lateral view. For nomenclature of *L. longispinis* see p. 12 *et seq.*

come to resemble those of *L. calcarifer* more closely, the resemblance increasing with the size of the skull. Katayama (1956) figures the neurocranium from a *L. calcarifer* of 28·6 cm S.L.; judging from this figure there is little difference between a skull of that size and one from a *L. niloticus* of comparable length. Seemingly the orbital and precommissural skull proportions change much more rapidly in *L. calcarifer*; compare, for example, the 103 mm skull of *L. calcarifer* (S.L. *c.* 40 cm) with the 123 mm skull of *L. niloticus* (S.L. *c.* 48 cm) in Figs 3 and 2.

Compared with the four species from outside Lake Tanganyika, three endemic Tanganyikan species, *L. microlepis*, *L. mariae* and *Luciolates stappersi* (Figs 5–8) show a distinct narrowing of the skull (particularly the braincase), an elongation of the ethmoid region, and an angling of the parasphenoid relative to the basioccipital. The slope of the parasphenoid is steepest in *L. mariae* and least in *L. microlepis*, with *Luciolates* occupying an intermediate position in the series.

The fourth Lake Tanganyika endemic, *L. angustifrons* (Fig. 5), is, in most features of its neurocranial profiles, intermediate between the other endemic species and those from outside the lake. Nevertheless, it is clearly differentiated from the latter by

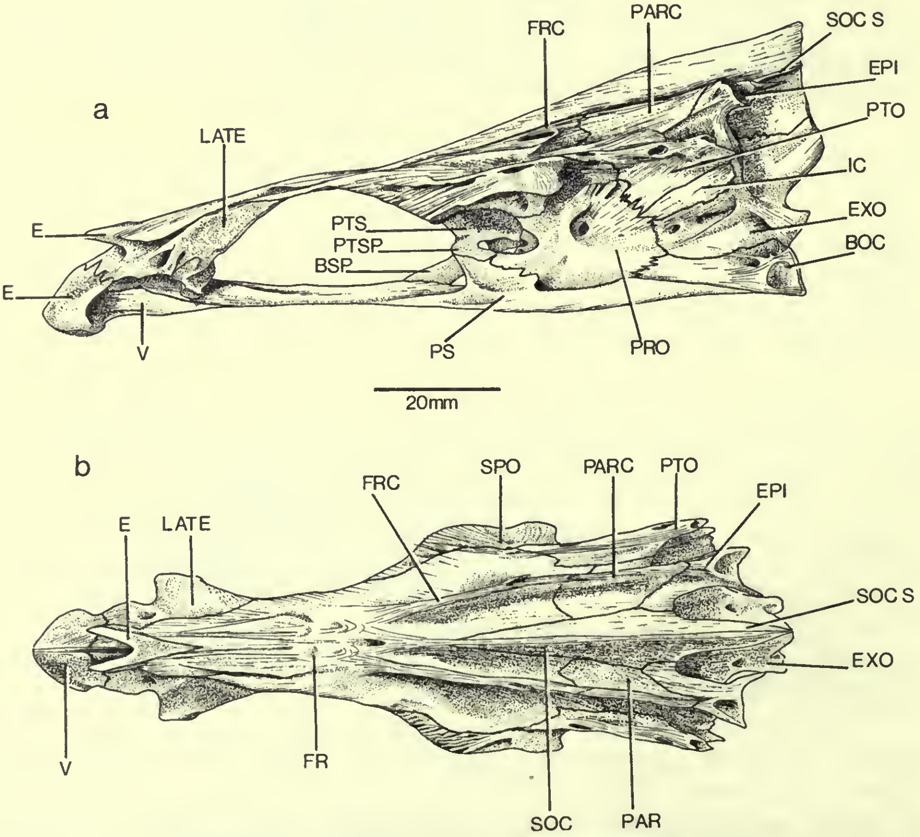


FIG. 5. *Lates angustifrons*. Neurocranium in: (a) left lateral view, (b) dorsal view.

the elongation of its ethmoid region and by the shape of its ethmoid bones, characteristics that unite it with the other endemic species from Lake Tanganyika (see below).

This elongation of the ethmovomerine skull region in all species of *Lates* (and *Luciolates*) from Lake Tanganyika immediately distinguishes the group (see Table 1), and argues strongly for their monophyletic origin. The concave posterior face of the lateral ethmoid in *L. angustifrons*, *L. microlepis*, *L. mariae* and *Luciolates stappersi*, as compared with members of the *L. calcarifer–L. niloticus* complex, has a distinct posterior slope (cf. Figs 2–4 with 5–8). Furthermore, and most strikingly, the lateral margins of the bone are much wider (or, as it appears in lateral view, much deeper) and have a pronounced downward slope. In the *L. calcarifer–L. niloticus* group the posterior margin of the lateral ethmoid is almost vertically aligned, and its lateral margins are narrow and horizontally aligned (cf. Figs 2–4 with 5–8). Once again it is *Luciolates* that shows the most profound modifications with, in this instance, *L. microlepis* showing the least modified condition and *L. angustifrons* and *L. mariae* (in that order) occupying the intermediate places in the series.

TABLE 1

Relative length of ethmovomerine region in various *Lates* spp., and in *Psammoperca waigiensis*

Species	Neurocranial[1] length (mm)	Ethmovomerine[2] length (mm)	Ethmovomerine length as % of neurocranial length	
Lates calcarifer	103·0	25·0	24·2%	Subgenus *Lates* (see p. 77)
L. niloticus	16·0	5·0	31·3%	
	76·0	21·5	28·3%	
	124·0	30·5	24·8%	
	228·0	60·5	26·7%	
L. macrophthalmus	32·0	8·5	26·5%	
L. longispinis	59·5	16·5	28·7%	
L. angustifrons	120·0	43·3	36·8%	Subgenus *Luciolates* (see p. 71)
L. mariae	26·0	10·0	38·5%	
	77·5	32·0	41·3%	
L. microlepis	44·0	18·0	41·0%	
L. stappersi	71·0	31·0	43·5%	
	71·0	32·5	45·8%	
	103·5	49·0	46·9%	
Psammoperca waigiensis	43·0	14·5	33·7%	

[1] Neurocranial length: measured directly from the anterior tip of the vomer to the posterior point on the lower margin of the basioccipital facet for the first vertebra.

[2] Ethmovomerine length: measured directly from the anterior point of the vomer to that point on the dorsicranium where the lateral ethmoid-prefrontal passes under lateral margin of the frontal.

There is little interspecific variation in the morphology of the lateral ethmoids of *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis* (see Figs 2–4).

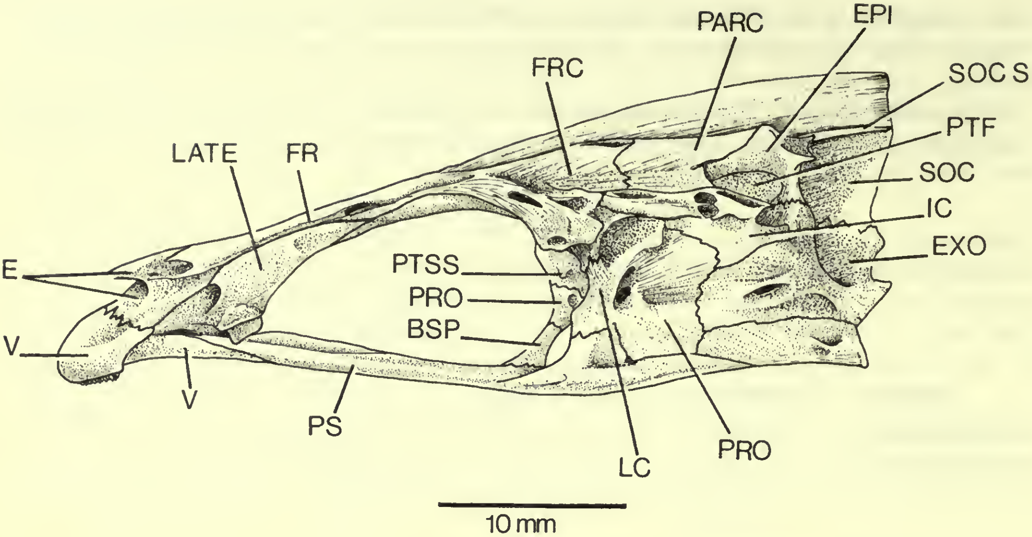


FIG. 6. *Lates microlepis*. Neurocranium in left lateral view.

All *Lates* species, and *Luciolates*, have three facets on each lateral ethmoid ; two, ventrally placed, are for articulation with the palatine, and the third (situated dorsolaterally above the posterior palatine facet) for articulation with the first circumorbital bone (lachrymal). The facets are less well defined in the Tanganyika species, and are most poorly differentiated in *Luciolates*.

A noticeable feature of the skull in *L. calcarifer*, *L. niloticus* and, to a slightly lesser degree, in *L. angustifrons* is the way in which the anterior wall of the neurocranium (i.e. the prootic, pterosphenoid and ascending arm of the parasphenoid) are extended forward beyond the level of the lateral commissure (Figs 2, 3 & 5) ; in *L. calcarifer* and *L. niloticus* the tunnel-like ventral part of this extension surrounds all but the anterior half or more of the basisphenoid. This feature is emphasized when the skulls of these species are compared with those of *L. mariae*, *L. microlepis* and *Luciolates stappersi*, species in which there is only a slight prolongation of the neurocranial wall beyond the level of the lateral commissure (cf. Figs 2, 3 & 5 and 6–8). The situation in *L. macrophthalmus* and *L. longispinis* is virtually intermediate between those in the other two groups. (See Table 2 and Fig. 4.)

Closer examination of the precommissural extension in specimens of *L. calcarifer* (neurocranial length, ncl., 103 mm), *L. niloticus* (ncl., 75 mm and above) and *L. angustifrons* (ncl., 120 mm) reveals the existence of a pterosphenoid pedicle which, through its contact with the parasphenoid anteriorly and the outer lip of a horizontal groove in the prootic, forms a semi-tubular bridge over the oculomotor and profundus nerves and the internal jugular vein (Figs 9 & 10). Rognes (1973) has called a similar stucture in labrids an internal jugular bridge, and that name will be used here.

TABLE 2

Precommissural skull proportion in *Lates* and *Psammoperca*

Species	Neurocranial[1] length (mm)	Precommissural[2] skull length (mm)	Precommissural length as % of neurocranial length
Lates calcarifer	103·0	25·0	24·2%
L. niloticus	76·0	10·0	13·1%
	124·0	22·0	17·7%
L. longispinis	59·5	6·0	10·1%
L. macrophthalmus	32·0	3·0	9·4%
	74·0	10·0	13·5%
L. angustifrons	120·0	14·0	11·7%
L. stappersi	71·0	3·5	4·9%
	103·5	6·0	5·8%
Psammoperca waigiensis	43·0	2·5	5·7%

[1] See Table 1 (p. 19).

[2] Precommissural skull length: measured directly from the anterior margin of the lateral commissure to the anterior margin of the ascending limb of the parasphenoid.

The relative contributions of the prootic and parasphenoid bones to the internal jugular bridge show marked intraspecific variability, and usually differ on either side (see Fig. 9c–d). The parasphenoid contribution is always the least important, the major part of the ventral wall (and the entire groove) coming from the prootic, and the dorsal and lateral walls from the pterosphenoid pedicle. Except in the small *L. niloticus* skulls examined (see below) there is always some contact between the three bones at the orbital (i.e. front) margin of the bridge. Since the smallest available skulls of *L. calcarifer* and *L. angustifrons* measure 103 mm and 120 mm long respectively, no comment can be made on the interrelationship of these bones in small individuals of those species.

Apparently correlated with the degree of pterosphenoid development and the development of the precommissural braincase is the extent to which the autosphenotic is prolonged anteriorly. The correlation is a positive one in species with an extensive precommissural braincase and a well-developed pedicle (i.e. *L. calcarifer* and *L. niloticus*). The anterior extension of the autosphenotic is least marked in *Luciolates stappersi*, *L. mariae* and *L. microlepis*, and is of intermediate length in *L. angustifrons*, *L. macrophthalmus* and *L. longispinis*.

Before describing and comparing the precommissural crania for all *Lates* and *Luciolates* species, it is necessary to consider the ontogenetic changes involved in the production of an adult *L. niloticus*-type pterosphenoid pedicle and internal jugular bridge.

The smallest *L. niloticus* skulls examined (12 mm long) have no noticeable precommissural extension of the braincase; the parasphenoid does not contact the pterosphenoid and there is no bony bridge over the nerves and blood vessel (Fig. 9a). At the ontogenetic stages represented by those skulls there is also no obvious

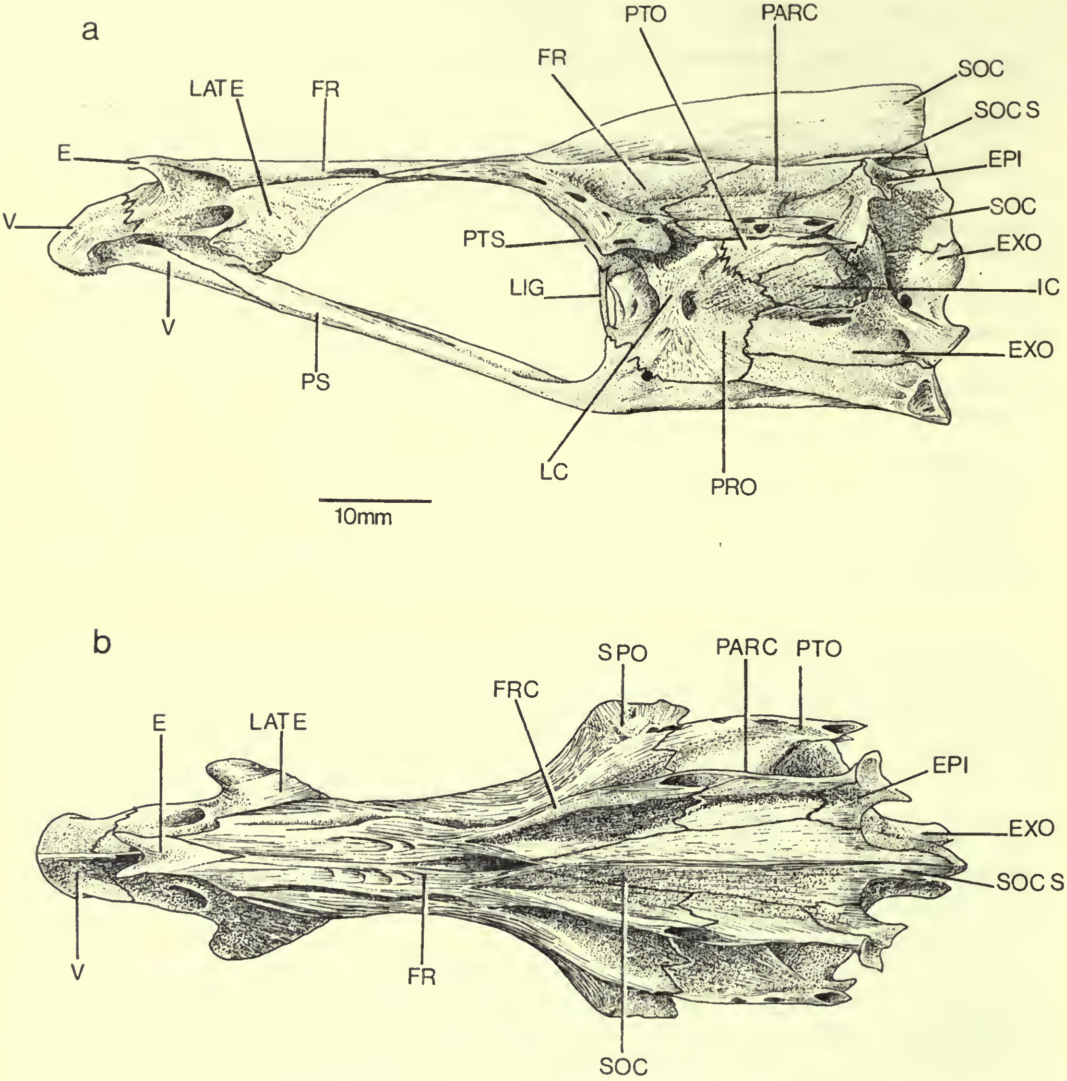

a
PTO
PARC
FR
SOC
LAT E
FR
SOC S
E
EPI
V
SOC
PTS
EXO
LIG
IC
V
EXO
PS
LC
PRO
10mm
b
S PO
PARC
PTO
FRC
E
LAT E
EPI
EXO
SOC S
V
FR
SOC

Fig. 7. *Lates mariae.* Neurocranium in : (a) left lateral view, (b) dorsal view.

pterosphenoid pedicle, but a narrow ligament runs from the lower, anterior part of the pterosphenoid to the outer rim of the weakly developed prootic groove lying below the internal jugular vein (Fig. 9a) ; in effect, the ligament occupies the position later taken by the pterosphenoid pedicle arm of the internal jugular bridge. At its dorsal base, the ligament is attached to a small spur of bone on the pterosphenoid, which I would interpret as an incipient pedicle.

In progressively larger skulls (i.e. to a length of 76 mm), there is a gradual development and down-growth of the pterosphenoid pedicle, and of a dorsally directed

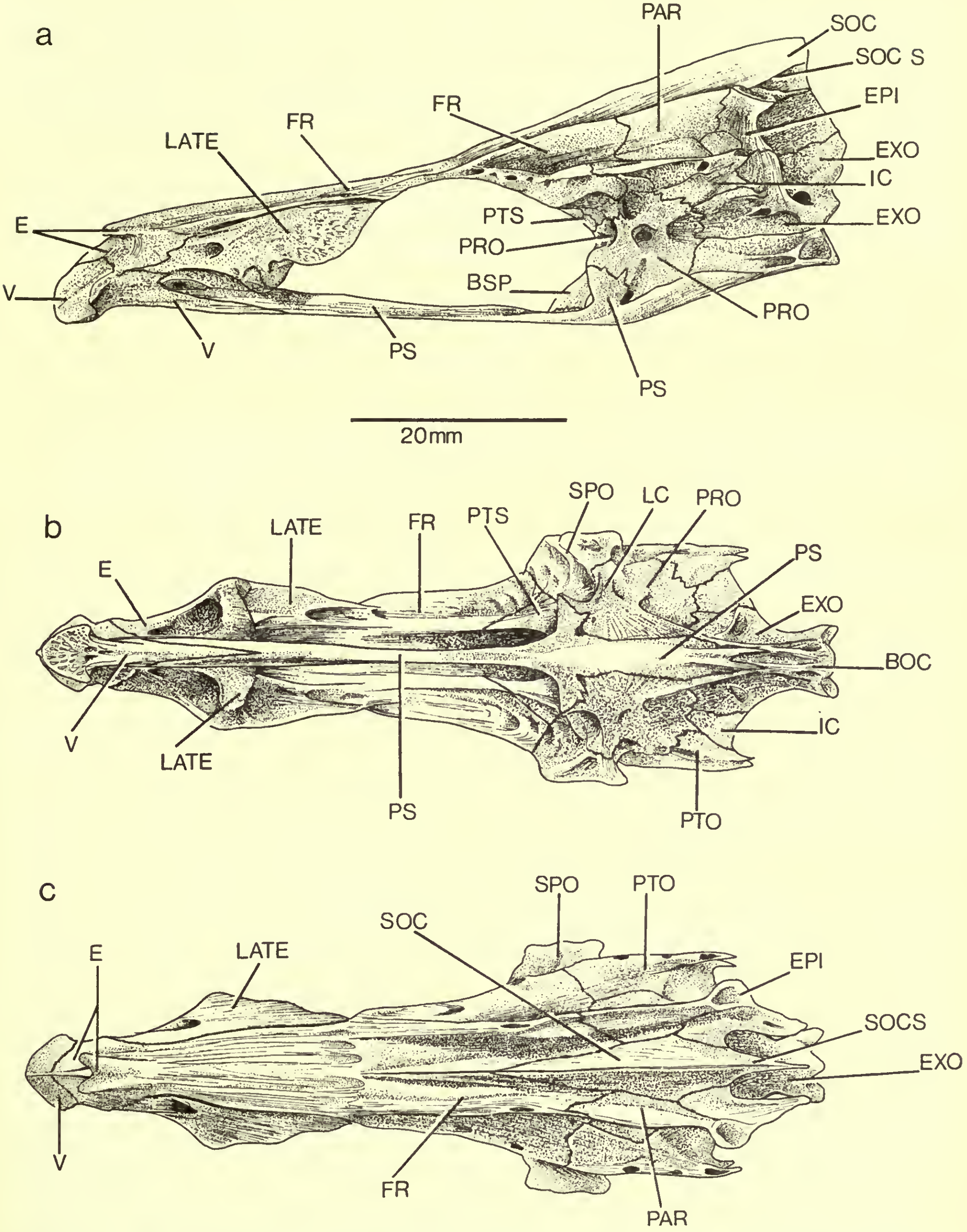

a
PAR
SOC
SOC S
EPI
FR
FR
LATE
EXO
IC
EXO
E
PTS
PRO
BSP
PRO
V
V
PS
PS
20mm
b
SPO
LC
PRO
LATE
FR
PTS
PS
E
EXO
BOC
IC
V
LATE
PS
PTO
c
SPO
PTO
SOC
E
LATE
EPI
SOCS
EXO
V
FR
PAR

Fig. 8. *Lates stappersi.* Neurocranium in: (a) left lateral view, (b) ventral view, (c) dorsal view. For details on the altered generic placement of this species (previously *Luciolates stappersi*) see p. 50.

spur-like development from the prootic lateral to the internal jugular groove. As a consequence of these growth patterns (and a dorsal extension of the ascending parasphenoid arm) an at first narrow (Fig. 9b), but gradually broadening, bony ridge is formed over the internal jugular vein and the associated oculomotor and profundus nerves. Concurrently, there is a gradual forward growth of the precommissural region of the skull.

A *L. niloticus* skull 76 mm long has the pterosphenoid pedicle and precommissural skull developed to an extent comparable with that in a *L. angustifrons* skull 120 mm long. Growth of the precommissural skull wall in *L. niloticus* continues beyond this

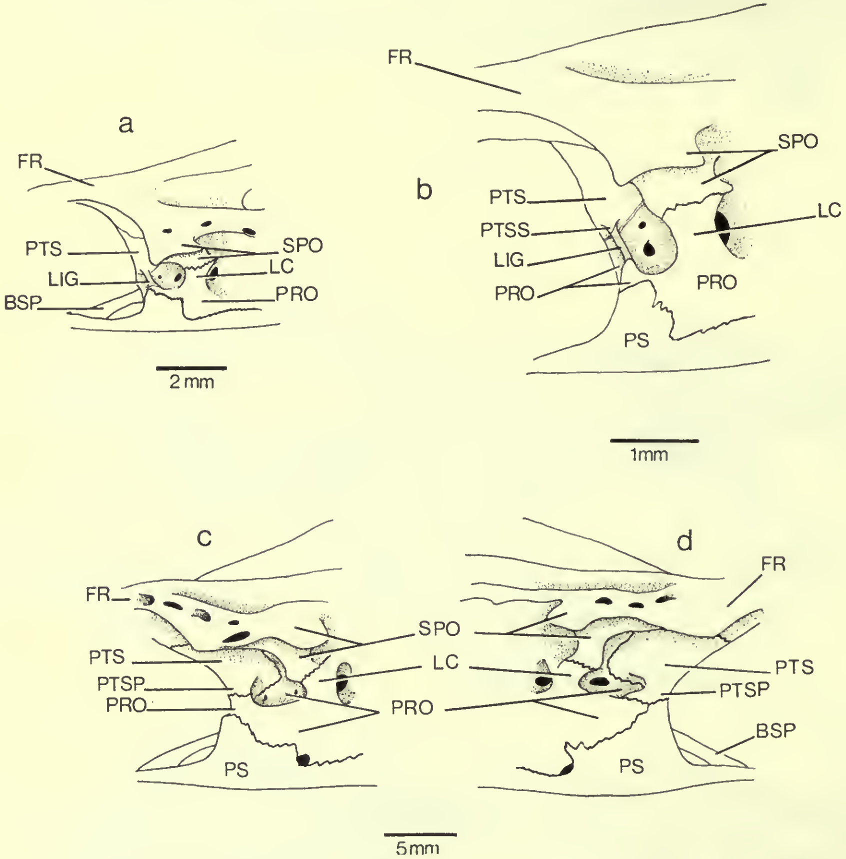


Fig. 9. Outline figures of internal jugular bridge, pterosphenoid pedicle and precommissural skull to show in : (a) & (b) growth changes in *L. niloticus* and in : (c) & (d) variability in the bridge of a single specimen of *L. longispinis*. (a) *Lates niloticus* ; left lateral view, neurocranial length 12 mm. Note ligamentous connection between spur of pterosphenoid and process on prootic. (b) *L. niloticus* ; left lateral view, neurocranial length 16 mm. Note downgrowth of pterosphenoid spur (= pedicle) to join prootic process. (c) & (d) *L. longispinis*. Left and right sides of skull showing variation in the interrelationships of bones contributing to the internal jugular bridge. Note direct pterosphenoid–parasphenoid contact in (d).

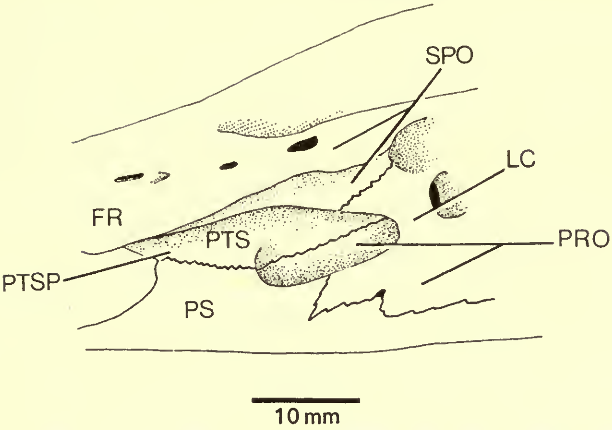


FIG. 10. *Lates calcarifer*. Outline figure to show relative hyperdevelopment of precommissural skull (left lateral view), especially the pterosphenoid pedicle and internal jugular bridge. Compare with Figs 9(c) & (d), 5(a), 2(a). From a skull of 10·3 cm neurocranial length.

point ; in a skull 124 mm long it has attained, however, the overall morphology and proportions seen in the largest skull examined (230 mm long).

Unfortunately no *L. angustifrons* skulls longer than 120 mm could be obtained so it has not been possible to determine the definitive form in that species. However, to judge from the totality of interspecific differences seen in skulls of about the same size it seems unlikely that this region of the neurocranium in *L. angustifrons* ever attains the proportions found in either *L. niloticus* or *L. calcarifer* (see above, p. 21).

As was noted earlier (p. 20), the precommissural skull region in *L. macrophthalmus* and *L. longispinis* is less well developed than in adult *L. calcarifer* and *L. niloticus*. It must, however, be remembered that members of the two former species reach a much smaller adult size (Worthington, 1929, 1932).

In a *L. macrophthalmus* skull 74 mm long (from a fish of 275 mm S.L.) the internal jugular bridge and the pterosphenoid pedicle have about the same degree of development as in a 76 mm long skull of *L. niloticus* (S.L. *c.* 290 mm) or a 120 mm long skull of *L. angustifrons* (S.L. *c.* 350 mm) ; the situation is similar in a slightly larger individual of *L. macrophthalmus* (320 mm S.L., neurocranial length 110 mm) Both specimens have a narrow parasphenoidal contribution to the bridge which is otherwise formed mainly from the pterosphenoid pedicle and the prootic spur. The smallest *L. macrophthalmus* skull examined (32·5 mm long, from a fish of 110 mm S.L.) shows a degree of development comparable with that in a *L. niloticus* skull only 16 mm long ; namely, a ligamentous bridge, and the pterosphenoid pedicle manifest only as a small spur of bone (Fig. 9a).

Conditions in *L. longispinis*, as seen in a skull 59 mm long (from a fish *c.* 250 mm S.L.), are close to those in the 74 mm skull of *L. macrophthalmus*, but the bridge is a little narrower. In a larger skull (70 mm long from a fish 275 mm S.L.) the bridge and pedicle, and the precommissural skull proportions are similar to those in the

76 mm skull of *L. niloticus* described above (p. 24), with a distinct pedicle and, at least on one side of the skull, a parasphenoidal contribution to the internal jugular bridge (Fig. 9d); on the left side of this specimen, the ascending parasphenoid limb fails to reach the level of the upper lateral margin of the prootic (Fig. 9c).

It would seem, then, that the internal jugular bridge and the precommissural skull in both *L. longispinis* and *L. macrophthalmus* are comparable with those in similar-sized skulls of *L. niloticus*, or are perhaps a little less advanced in some individuals. In other words, the adult skull of *L. macrophthalmus* and *L. longispinis* retains at least some of the pre-adult features of *L. niloticus*.

A really marked reduction in the adult precommissural braincase and in the pterosphenoid pedicle and internal jugular bridge is seen in the skulls of three Lake Tanganyika taxa, namely *L. mariae, L. microlepis* and *Luciolates stappersi*. (This region of the skull is also relatively reduced, as compared with *L. niloticus*, in the fourth Tanganyika species, *L. angustifrons*, see pp. 20–25 above.)

In none of these three species does the parasphenoid contact the pterosphenoid, always being separated from that bone by the prootic (Figs 6–8). No trace of a pterosphenoid pedicle, even as a low ridge, is detectable in the three *Luciolates stappersi* skulls I have examined (neurocranial lengths 71 (f. 2) and 113 mm), but a low ridge was found in the largest of the three *L. mariae* skulls (26·0, 77·5 and 104·0 mm long).

A similar ridge is developed on the right but not the left pterosphenoid of a 44 mm long skull of *L. microlepis*. A larger skull (95 mm) of *L. microlepis*, however, has a well-developed, broad-based but distally narrowed pedicle which reaches almost to the level of the prootic spur (Fig. 6). It is connected to the prootic spur by a short section of what appears to be ossified ligament.

Thus, of these three species, *L. microlepis* is the only one in which the pterosphenoid pedicle makes a significant contribution to the internal jugular bridge. Even in the largest skulls of *L. mariae* and *Luciolates stappersi* there is only a ligamentous bridge, a condition directly comparable with that in the smallest specimens of *L. niloticus*, except that in the Tanganyika fishes the ligament appears to be ossified. In other words, the precommissural braincase in large specimens of *L. mariae* and *Luciolates stappersi* (standard lengths 390 and 415 mm respectively) is like that in *L. niloticus* of about 60 mm standard length, while that of a *L. microlepis* 390 mm standard length is comparable with a *L. niloticus* of about 130 mm S.L.

The pterosphenoid–prootic ligament found in juvenile *L. niloticus* and adults of Tanganyika taxa described above is readily separated from both its bones of attachment. Thus it seems unlikely that it is truly part of the pterosphenoid pedicle. Presumably the ligament is replaced by the pedicle as it grows down to meet the spur from the outer rim of the prootic groove. The large *L. microlepis* specimen noted above represents a late phase in this developmental sequence, the small *L. macrophthalmus* (ncl., 32·5 mm; p. 25) an early phase, and the adult condition in *L. niloticus, L. calcarifer* and *L. angustifrons* the terminal state.

An internal jugular bridge is of sporadic and phyletically widespread occurrence amongst living teleosts. Rognes (1973) gives detailed accounts of the bridge in labrine Labridae, and reviews records of its occurrence in other groups. I can confirm its presence in certain ostariophysans (*Alburnus* ; see also Holmgren & Stensiö, 1936, for *Abramis*), certain scorpaeniforms (*Enophrys bison*, *Scorpaena scrofa*, *Trigla hirudo*, see also Allis, 1909 ; Allen [1905] describes a bridge in *Ophidion* [Hexagrammidae]), and in several percoids (*Epinephelus* species [but not other serranids], *Stizostedion volgensis*, *Perca fluviatilis* [but not, apparently, in *Gymnocephalus*]), and in some sphyraenoids (*Sphyraena* sp.).

In the majority of cases where a bridge is present, it is of the type found in juvenile *L. niloticus*, namely a ligament (generally ossified) joining a reduced pterosphenoid pedicle to a process developed on the prootic (see above, p. 21). Only in *Enophrys bison* is a bridge of the *L. angustifrons* type present.

This list, based on samples taken from the families represented in the dry skeleton collection of the British Museum (Natural History), cannot by any means be considered complete, especially since the bridge is not always preserved in dry skeletons. Nevertheless, it is interesting to find that in none of the beryciform skeletons at my disposal is there any indication of a bridge nor even of the pterosphenoid pedicle (which is usually obvious even if the ligamentous part of the bridge is missing). Neither a bridge nor a pterosphenoid pedicle was noted in any of the Mesozoic beryciforms described by Patterson (1964).

Superficially, *Salmo trutta* has what appears to be an internal jugular bridge, but closer inspection shows that it is formed entirely within the prootic. Thus it would seem to be homologous with the 'prelateral commissure' described by Rognes (1973) in the labrid *Ctenolabrus exoletus* (see Rognes, op. cit., fig. 59).

The pterosphenoid pedicle has a long history in actinopterygian fishes, being well developed in some leptolepids and pholidophorids, in *Amia* and its fossil relatives *Sinamia* and *Ellenes*, and at least partially developed in some palaeoniscids (Patterson, 1975). As Patterson (op. cit., p. 409) observes : '. . . It is therefore likely that a pterosphenoid pedicle of some sort, or at least the potentiality to develop such a structure is a primitive actinopterygian feature.'

Since the pterosphenoid pedicle is an integral part of the internal jugular bridge (see above) and because this bridge is of widespread occurrence among teleosts, one may conclude that the bridge too is a primitive feature.

The absence or great reduction of the bridge and pedicle in certain *Lates* species can, therefore, be interpreted as an apomorphic feature, at least when individuals of these species attain a size at which the bridge would otherwise be present in related taxa. *Lates macrophthalmus* and *L. longispinis* (both species with reduced bridges) are examples of the situation where maximum adult size is about equal to that in preadult *L. niloticus* and *L. calcarifer* ; at that size, specimens of *L. niloticus* (and presumably *L. calcarifer*) have a poorly developed bridge. Thus, it is probably correct to consider *L. macrophthalmus* and *L. longispinis* as plesiomorphic with respect to the bridge character.

Hyopalatine arch and the preoperculum (Figs 11 & 12)

Apart from slight proportional changes in, particularly, the length of the palatine and ectopterygoid bones of the Tanganyika species, there is little interspecific variation in the hyopalatine arch of *Lates* species (see Figs 11 & 12).

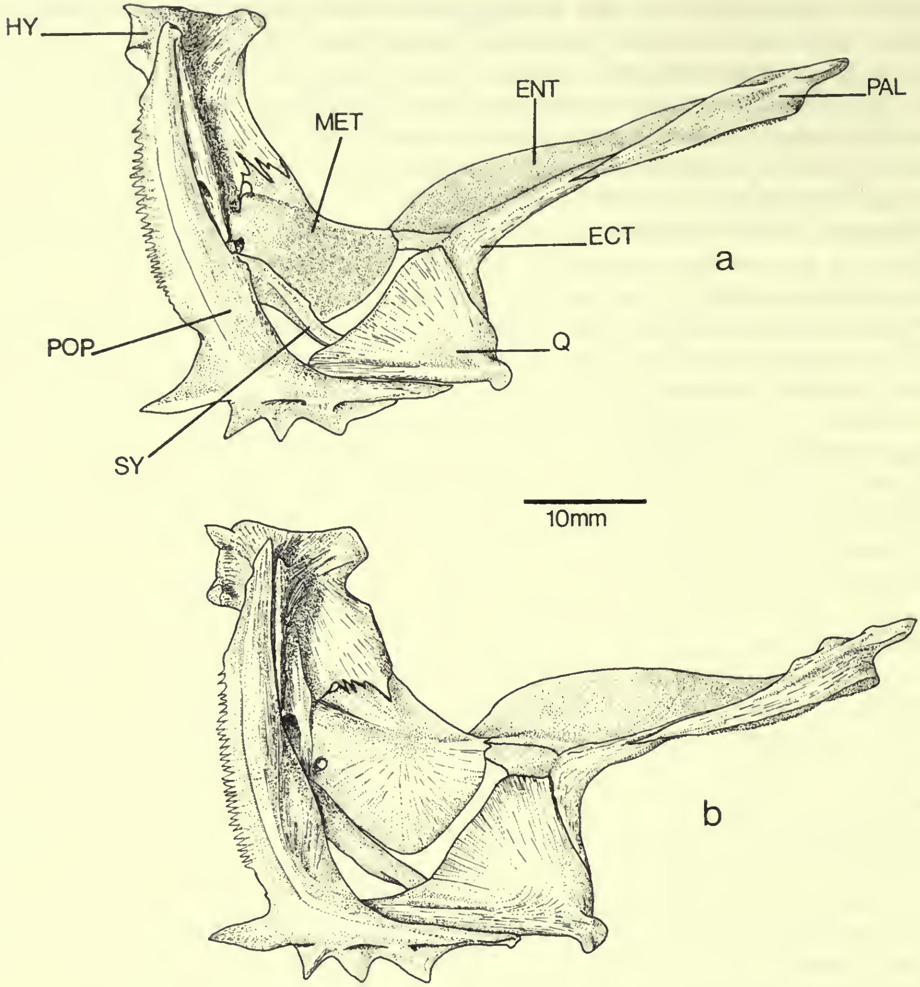


FIG. 11. Hyopalatine arch, right (including preoperculum) in lateral view of (a) *Lates mariae*, (b) *L. niloticus*.

The hyomandibula has two well-defined articulatory facets interconnected by a thin lamina of bone.

The metapterygoid has a strong sutural union with the hyomandibula and with the posterior tip of the expansive endopterygoid. There is no true metapterygoidal lamina (*sensu* Katayama, 1956, and Gosline, 1966) but a slight ridge is detectable in the position where a lamina would occur; also, in many species there is a small foramen (or fenestra) in the metapterygoid at the postero-dorsal end of the ridge. I would interpret these structures as the remnants of a greatly reduced metapterygoidal lamina.

Fine viliform teeth cover the entire ventral surface of the palatine. A similarly shaped (i.e. elongate ovoid) tooth patch occurs on the medial aspect of the anterior arm of the ectopterygoid, sometimes extending a short way onto the vertical arm of that bone as well.

The autopalatine is a fairly stout bone. Anteriorly, on its medial face are two well-defined articulatory surfaces for contact with the ethmoid ; dorsally there is a weakly demarcated facet for articulation with the lateral ethmoid. A panhandle-like, cartilage-tipped projection from the upper surface of the palatine provides articulation between this bone and the maxilla.

In most details, including the presence of a reduced metapterygoidal lamina, the hyopalatine arch of *Luciolates* resembles that of *Lates*, particularly the Lake Tanganyika species of the genus. However, all the bones (especially the endopterygoid) are thinner and the palatine is less robust, with poorly demarcated articulatory facets. The palatine tooth patch is much narrower in *Luciolates*, and there is a great

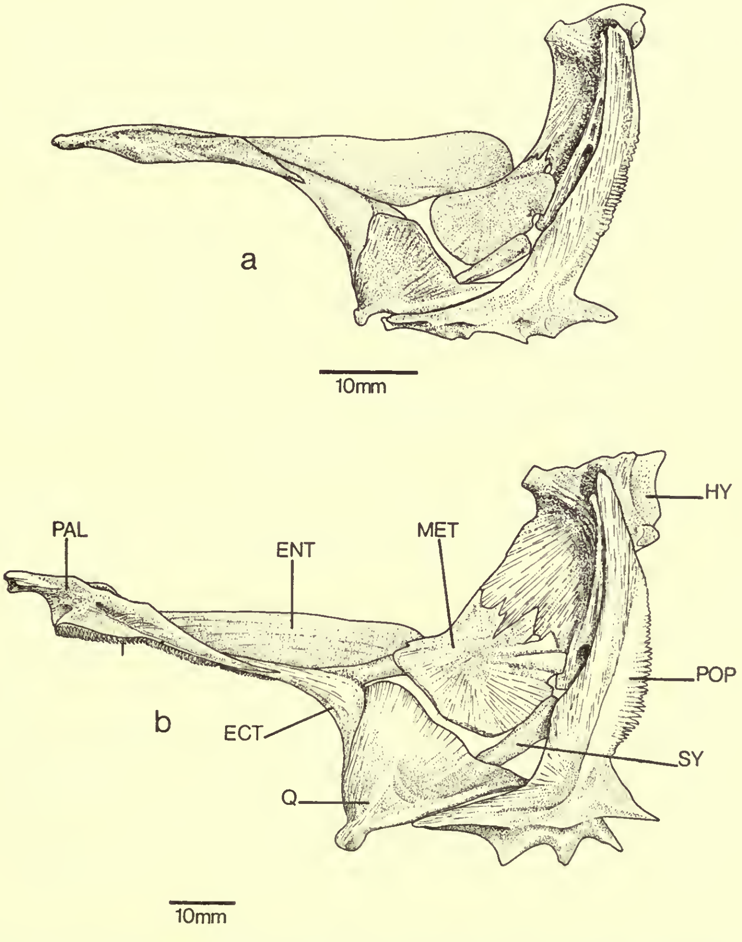


FIG. 12. Hyopalatine arch, left side (including preoperculum) in lateral view of (a) *Lates stappersi*, (b) *L. angustifrons*.

reduction in the area of the ectopterygoid teeth, the tooth-patch being either reduced to a small oval near the ectopterygoid-palatine articulation or it is completely absent. In one of the three skeletons examined the tooth-patch was present on one side only.

Like the hyopalatine arch, the preoperculum in *Lates* shows little interspecific variation, although it does show some intraspecific variability. The entire posterior margin of the vertical limb, except for a short length near its ventral angle, is finely serrate, the individual serrae are slender, sharp-pointed and tall. In very large specimens of *L. niloticus* (> 150 cm S.L.), the serrations are considerably reduced in height, and consequently the posterior margin of the bone is merely irregular (see also Sorbini, 1973).

At the posterior angle between the horizontal and vertical preopercular limbs there is a large, posteriorly directed and triangular spine (Fig. 11) ; very rarely this spine is subdivided almost to its base, resulting in two narrower but still triangular spines. On the horizontal limb there are generally three triangular spines, each slightly shorter and narrower than the spine at the bone's posterior angle. In larger *L. niloticus* the spines become irregular in outline, relatively shorter, and may have rounded rather than acute points.

Although three preopercular spines are modal for all species but *L. macrophthalmus*, a fourth spine is sometimes developed either on one or both sides. Usually the extra spine is a distinct entity, but sometimes it appears merely to be a subdivision of one of the other spines. *Lates macrophthalmus* is apparently exceptional in having a high proportion of individuals with four spines (seven of the eleven specimens examined). The proportion of four-spined fishes amongst samples of the other species is : *L. calcarifer*, none out of 18 ; *L. niloticus*, 7 out of 31 ; *L. longispinis*, 3 out of 6 (a high proportion, approaching that of *L. macrophthalmus*, which may be a related taxon, see p. 13) ; *L. angustifrons*, none out of 14 ; *L. mariae*, 4 out of 20 ; *L. microlepis*, 2 out of 27.

The occurrence of four-spined individuals may be a population feature, hence my reservations about the seemingly unusual condition in *L. macrophthalmus*. All but one of the *L. niloticus* specimens with four spines came from a single sample (incidentally, the largest available for *L. niloticus* and one much larger than was available for any other species).

Luciolates stappersi (Fig. 12a) also has a serrated posterior margin to the vertical preopercular limb, but here the serrations are lower and less well defined (in this respect resembling the condition in 16–20 mm standard length *L. niloticus*). The spine at the preopercular angle is always present and prominent, although it is somewhat finer than in any *Lates* species. The horizontal limb may have three large and relatively short spines, but specimens with two or three groups of very small spines, or even what amounts to a crenellated border, are common. The incidence of bilateral asymmetry in the type of spination is also high.

In both *Lates* and *Luciolates* the preopercular lateral line canal is completely bone enclosed, with its pores confined to the horizontal limb.

Although a serrated or otherwise ornamented vertical preopercular limb is of common occurrence amongst the lower percoids (e.g. in the Serranidae), the presence of large and discrete spines on the horizontal limb and at its angle is extremely rare (*Percalates* and *Siniperca* [Serranidae] are, as far as I can determine, the only taxa having the same type of preopercular ornamentation as *Lates*). A similar generalization can be made for the lower percomorphs (*sensu* Rosen, 1973; for example, the 'Beryciforms'). Thus, it seems reasonable to conclude that the ventral preopercular ornamentation in *Lates* (and probably other centropomids as well, see below) is a derived condition (see also Rosen, 1973 : 469). *Luciolates* too can be included in this generalization, the condition here being interpreted as the secondary simplification of a derived condition mimicking a plesiomorphic one.

Circumorbital bones (Figs 13a–d)

The greater part of the ventral margin to the first circumorbital bone (the lachrymal) is finely serrated in all *Lates* species; only a short anterior part is smooth. In all species the entire margin of the second circumorbital is also serrated.

The infraorbital lateral line canal in *Lates* and in *Luciolates* is enclosed throughout its length, communicating with the exterior through five pores in the lachrymal, one anteriorly on the third circumorbital bone, and through other pores found between successive bones in the series.

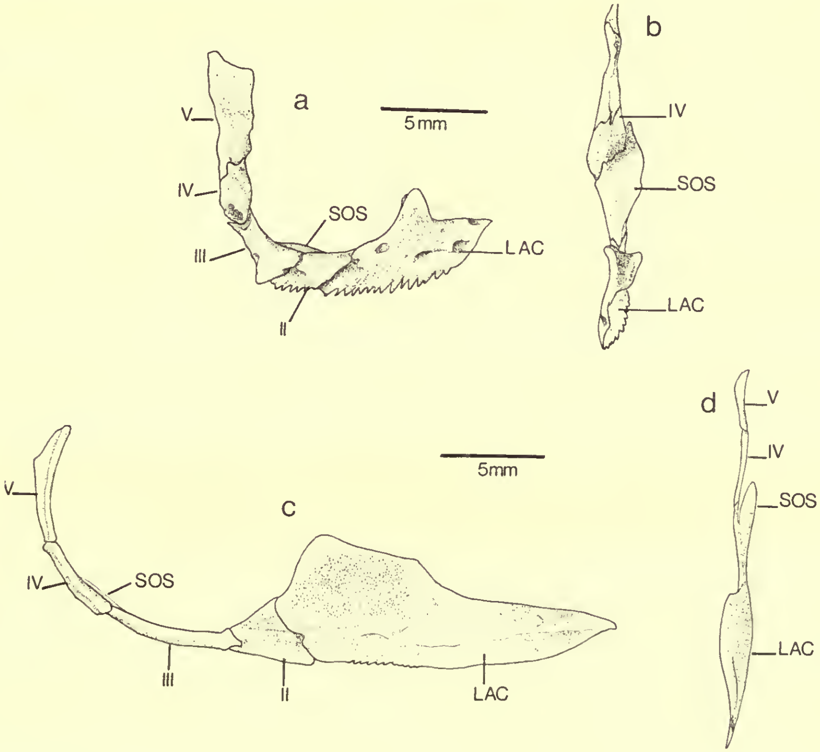


Fig. 13. Circumorbital bones (right side) in: (a) & (b) *Lates niloticus*, and in: (c) & (d) *L. stappersi*; (a) and (c) lateral view, (b) and (d) viewed dorsally and somewhat anteriorly.

All species (including *Luciolates stappersi*) have a well-defined facet developed at about the middle of the upper lachrymal margin ; it articulates with a similar facet on the lateral ethmoid.

There is a general similarity in the shape of the first two circumorbital bones in all *Lates* species, although the three species from Lake Tanganyika (*L. angustifrons*, *L. mariae* and *L. microlepis*) have a slightly more elongate lachrymal. These species (except *L. angustifrons*) also differ from *L. niloticus*, *L. calcarifer*, *L. macrophthalmus* and *L. longispinis* in having a relatively more elongate fifth circumorbital, and in having much narrower bony flanges developed from the ventral contours of the cylindrical canal-bearing portions of the third, fourth and fifth bones.

Greatest departure from the *L. niloticus–L. calcarifer* situation is seen in the reduced size of the subocular shelf in the Tanganyika species, again excepting *L. angustifrons* where the shelf is like that in *L. niloticus* and *L. calcarifer*, viz. a thin but broad bony plate that curves upwards from the third circumorbital to lie along the entire length of the fourth bone. In *L. microlepis* the subocular shelf is reduced in width, and just reaches upwards to the level of the articulation between the third and fourth circumorbitals ; in *L. mariae* there is a further and marked reduction in width, and the shelf barely reaches to the level of the articulation between the bones. Both species have the ventral flange on the third and fourth circumorbitals reduced to a thin flange.

These reductional trends are carried further in *Luciolates*, where the serrations on the lachrymal are very weak and are confined to about the posterior third of the bone ; serrations are completely absent from the second circumorbital. The facet for articulation with the lateral ethmoid is weakly developed, and its origin from the lachrymal is far less well defined than in the other species. The subocular shelf is, relatively, a little narrower than in *L. mariae*, but it does extend further up the fourth circumorbital (along about its lower third) ; see Fig. 13c–d. The depth of the ventral flange on the second to fourth circumorbitals is almost comparable with *L. mariae*, as is the flange on the fifth bone. In their gross morphology, the circumorbital bones in *Luciolates stappersi* are noticeably more elongate than those in any *Lates*, including the other Lake Tanganyika species. Apart from differences in the overall proportions of the first, third and fourth bones, the morphology of the entire series in an adult *Luciolates* of 105 mm standard length closely resembles that in a juvenile *Lates niloticus* 32 mm long.

Opercular bones (Figs 14a–b)

There is little variation in the operculum, suboperculum and interoperculum of *Lates* and *Luciolates*, apart from a slight relative elongation of the interoperculum in the Tanganyika species, especially *Luciolates*. In all taxa there is a well-defined, curved ridge on the medial face of the interoperculum against the upper, concave surface of which the proximal end of the epihyal articulates.

The operculum (Fig. 14a–b) is armed with a single stout spine formed from the posterior tip of the near-horizontal strut which runs backwards from the hyomanibular facet of the bone.

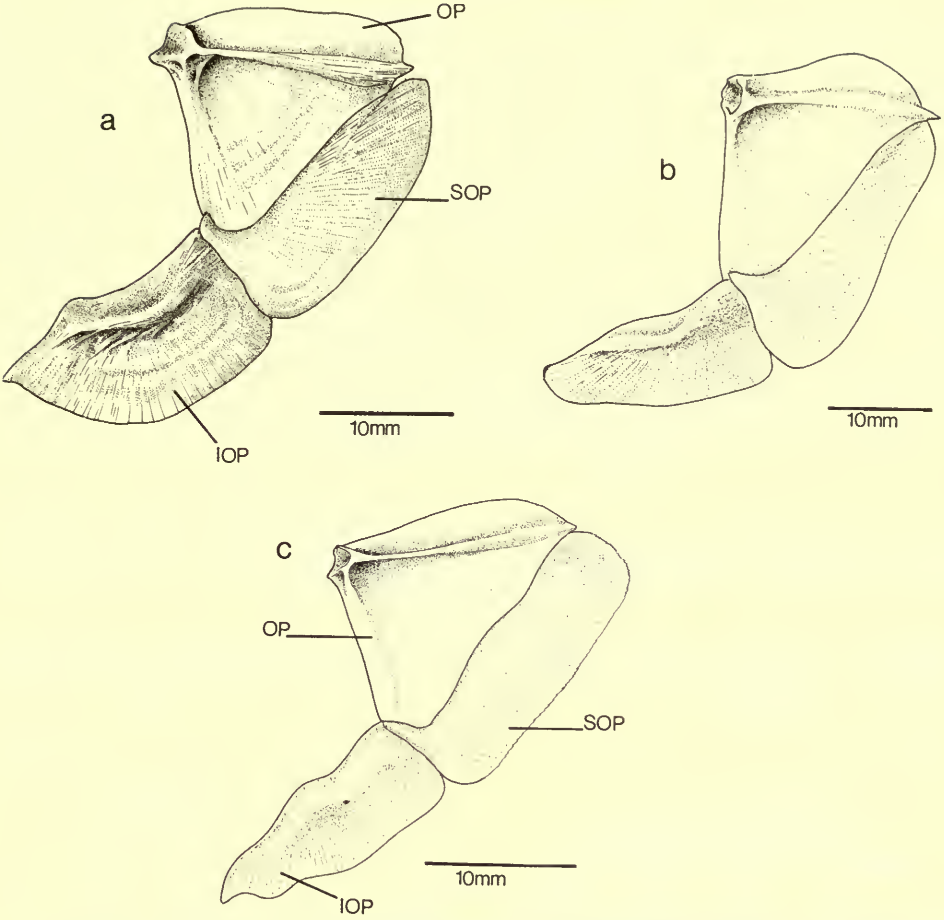


FIG. 14. Opercular series (medial aspect of bones from right side) in : (a) *Lates angustifrons*, (b) *L. stappersi*, (c) *Psammoperca waigiensis*.

A characteristic feature in all taxa is the thinness of the sub- and interopercular bones.

Jaws (Figs 15 & 16)

Both the maxilla and the premaxilla show little interspecific variation amongst *Lates* species, and are of the generalized percoid type. There is also little difference between *Lates* and *Luciolates* in the morphology of these bones. However, in *Lates* species the ascending process of the premaxilla is from 30 to 60 per cent higher than the articular process (apparently being lowest in the Lake Tanganyika species) ; it is only a little higher than the ascending process in *Luciolates stappersi*.

The premaxillary dentition in all *Lates* species is composed of numerous close-set rows of small conical to subconical teeth which form a villiform covering to the complete width of the bone over almost its entire length (Figs 15b–c).

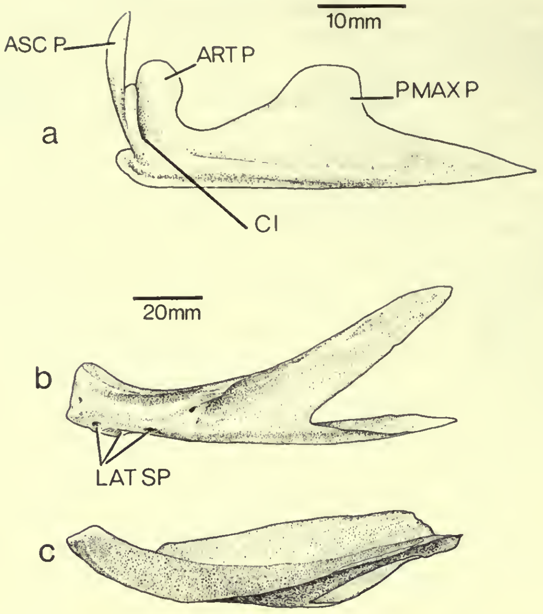

10mm
ASC P
ART P
PMAX P
a
CI
20mm
b
LAT SP
c

FIG. 15. *Lates niloticus*. (a) Premaxilla (left) lateral view. (b) Dentary (left) lateral view. (c) Dentary (left) occlusal view. (All from Greenwood & Howes, 1975.)

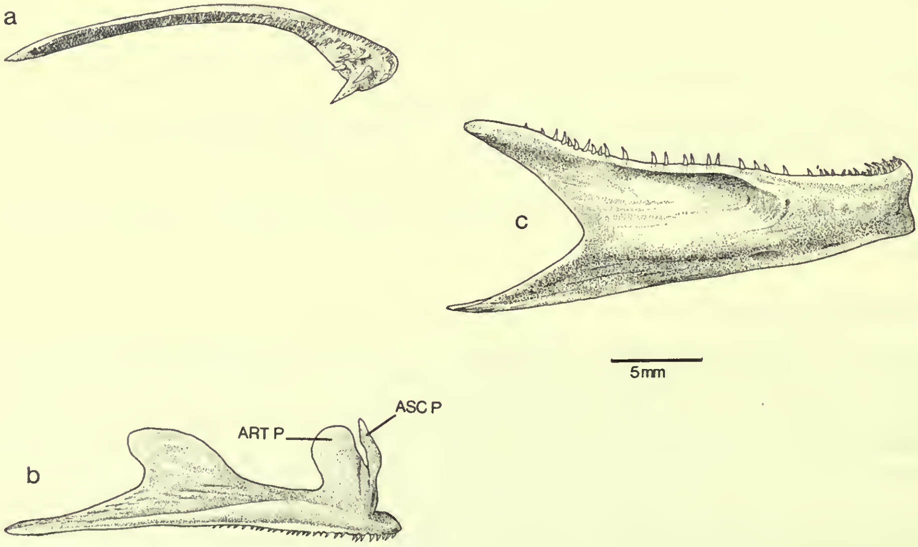

a
c
5mm
ASC P
ART P
b

FIG. 16. *Lates stappersi*. (a) Premaxilla (right), occlusal view. (b) Premaxilla (right), lateral view. (c) Dentary (right), lateral view.

Although most premaxillary teeth in *Luciolates stappersi* are like those in *Lates*, the species is noteworthy for the presence of at least one greatly enlarged and two slightly smaller caniniform teeth adjacent to the symphysial surface of the premaxilla ; a few neighbouring teeth may also be somewhat enlarged. In general the larger teeth are linearly arranged, with the largest one situated lingually.

The upper jaw elements in *Lates* and *Luciolates* show no derived characteristics and, of course, both genera retain the supramaxilla. The enlarged median teeth of *Luciolates*, however, would seem to be a derived feature.

Like the upper jaw, the lower jaw elements (dentary, anguloarticular and retroarticular) show little interspecific variation. In *Luciolates* the anguloarticular is relatively shallow, but otherwise has a typical '*Lates*' form.

The dentition of the dentary mirrors that on the premaxilla, except that in *Luciolates* the outermost tooth row is composed of noticeably larger and more clearly caniniform teeth, and there are no enlarged symphysial teeth.

Branchial skeleton (Figs 17–19)

The branchial skeleton in both *Lates* and *Luciolates* is of a generalized percoid type (see Rosen, 1973), and it shows few interspecific differences, apart from a relative

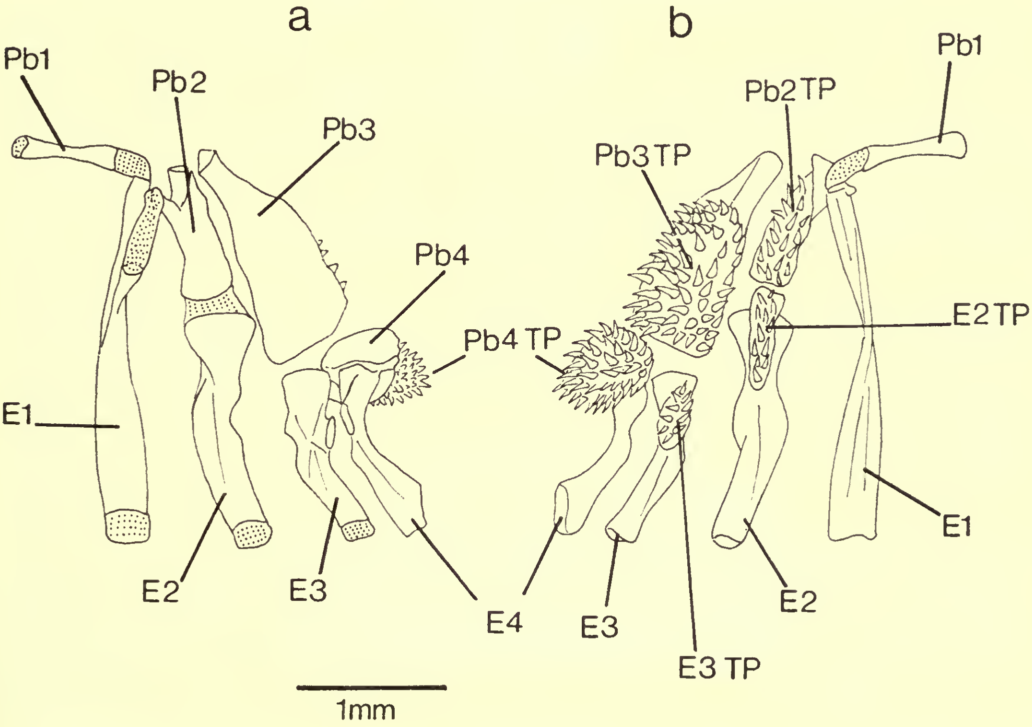


FIG. 17. *Lates niloticus*. Branchial skeleton, dorsal part (drawn from an alizarin preparation, 40 mm S.L.). (a) Dorsal aspect of left side. (b) Ventral aspect (left side) to show upper pharyngeal teeth and tooth plates.

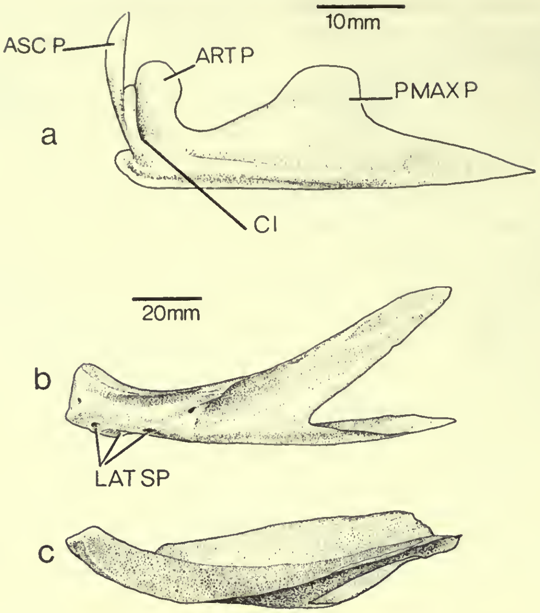

10mm
ASC P
ART P
PMAX P
a
CI
20mm
b
LAT SP
c

FIG. 15. *Lates niloticus*. (a) Premaxilla (left) lateral view. (b) Dentary (left) lateral view. (c) Dentary (left) occlusal view. (All from Greenwood & Howes, 1975.)

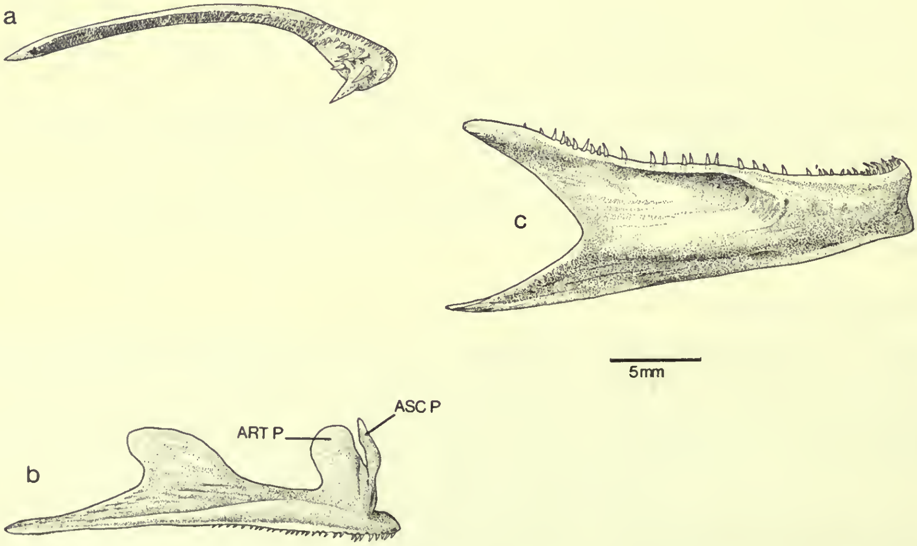

a
c
5mm
ASC P
ART P
b

FIG. 16. *Lates stappersi*. (a) Premaxilla (right), occlusal view. (b) Premaxilla (right), lateral view. (c) Dentary (right), lateral view.

Although most premaxillary teeth in *Luciolates stappersi* are like those in *Lates*, the species is noteworthy for the presence of at least one greatly enlarged and two slightly smaller caniniform teeth adjacent to the symphysial surface of the premaxilla ; a few neighbouring teeth may also be somewhat enlarged. In general the larger teeth are linearly arranged, with the largest one situated lingually.

The upper jaw elements in *Lates* and *Luciolates* show no derived characteristics and, of course, both genera retain the supramaxilla. The enlarged median teeth of *Luciolates*, however, would seem to be a derived feature.

Like the upper jaw, the lower jaw elements (dentary, anguloarticular and retroarticular) show little interspecific variation. In *Luciolates* the anguloarticular is relatively shallow, but otherwise has a typical '*Lates*' form.

The dentition of the dentary mirrors that on the premaxilla, except that in *Luciolates* the outermost tooth row is composed of noticeably larger and more clearly caniniform teeth, and there are no enlarged symphysial teeth.

Branchial skeleton (Figs 17–19)

The branchial skeleton in both *Lates* and *Luciolates* is of a generalized percoid type (see Rosen, 1973), and it shows few interspecific differences, apart from a relative

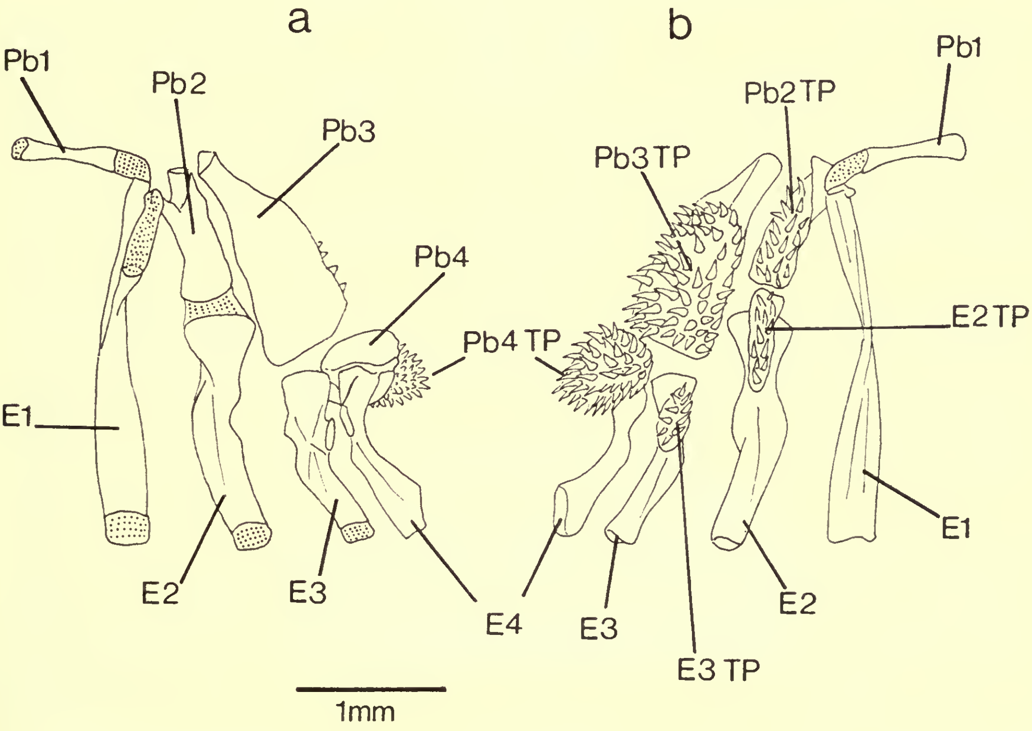


Fig. 17. *Lates niloticus*. Branchial skeleton, dorsal part (drawn from an alizarin preparation, 40 mm S.L.). (a) Dorsal aspect of left side. (b) Ventral aspect (left side) to show upper pharyngeal teeth and tooth plates.

elongate so that it overlaps the joint between the two bones. The plates associated with the third arch are generally the largest of the series, approach one another medially and cover a great deal of the third basibranchial.

In the one available branchial skeleton of *L. angustifrons* the individual plates appear to have fused together on the first two gill arches to form a long tooth plate on each side of the arch. A similar arrangement is seen in the alizarin preparation of a small (96 mm S.L.) *Luciolates stappersi*, but this specimen differs in other respects, especially in having a single, median plate on the third basibranchial and a small plate on each hypobranchial of that arch. The arches dissected from a much larger specimen (270 mm S.L.) have the plates of the third basibranchial narrowly separated medially, a long plate at the base of the second gill arch and a small plate intercalated between it and the basal plate of the first arch. Clearly, at least in this species, there can be quite considerable individual variability in the pattern of tooth plate distribution (see Nelson, 1969 : 500–501, for a description of variation in another percoid, *Pomatomus saltatrix* [Pomatomidae]).

Hyoid arch (Figs 20 & 21)

The hyoid arch in *Lates* and *Luciolates* is of a basal percoid type, with dorsal and ventral hypohyals, a large and complete 'berycoid' foramen and seven branchiostegal rays. There is remarkably little interspecific variability in the shape of this

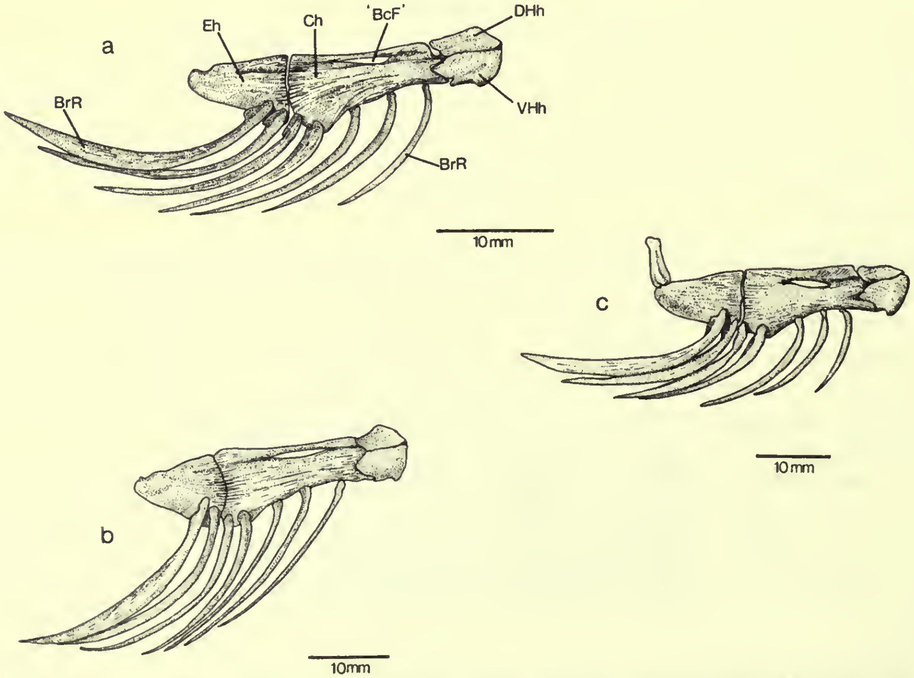


Fig. 20. Hyoid arch and branchiostegal rays (right side), viewed laterally, in : (a) *Lates stappersi*, (b) *L. mariae*, (c) *L. niloticus*.

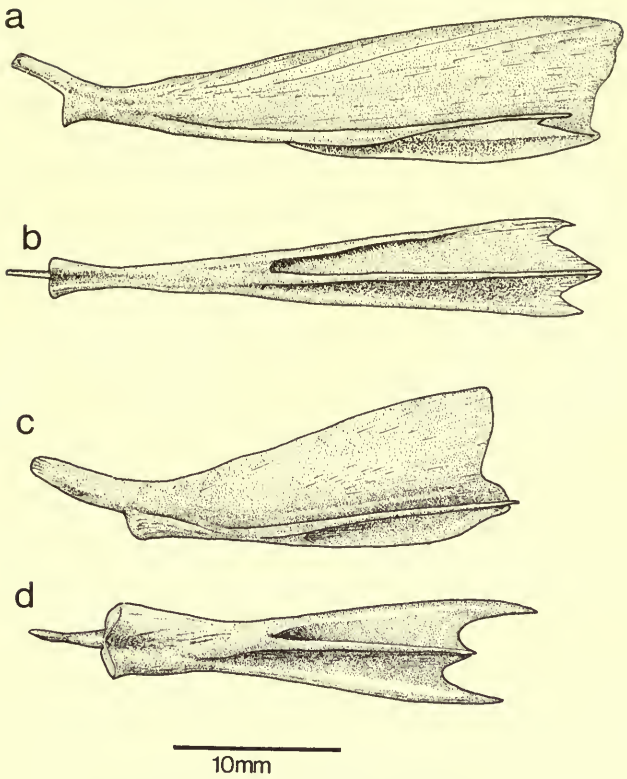


Fig. 21. Urohyal. (a) & (b) *Lates stappersi* (left lateral and ventral views respectively). (c) & (d) *L. angustifrons* (left lateral and ventral views respectively).

arch, without even, as might be expected, clear-cut proportional differences in the arches from species with elongate skulls (i.e. the Tanganyika species).

The first four branchiostegal rays articulate with the ceratohyal, the fifth with either the ceratohyal or at the cerato-epihyal suture, and the last two rays (the stoutest and broadest of the series) articulate with the epihyal. The first three rays contact the ventral face of the ceratohyal, the other four lie on the lateral aspect of the cerato- or epihyal. These latter rays have progressively broader heads, with the dorsal outline of the head on the last two, or occasionally three rays somewhat indented.

The basihyal is an elongate bone, spatulate in dorsal outline, and does not carry a tooth plate.

The urohyal (Fig. 21) is similar in all species, but is markedly more elongate in *Luciolates*, even when it is compared with the urohyal in the *Lates* species of Lake Tanganyika.

Pectoral girdle and associated bones (Fig. 22)

The pectoral girdle shows few interspecific or intergeneric differences, either in its overall proportions or in the shape of its individual bones. Judging from the only

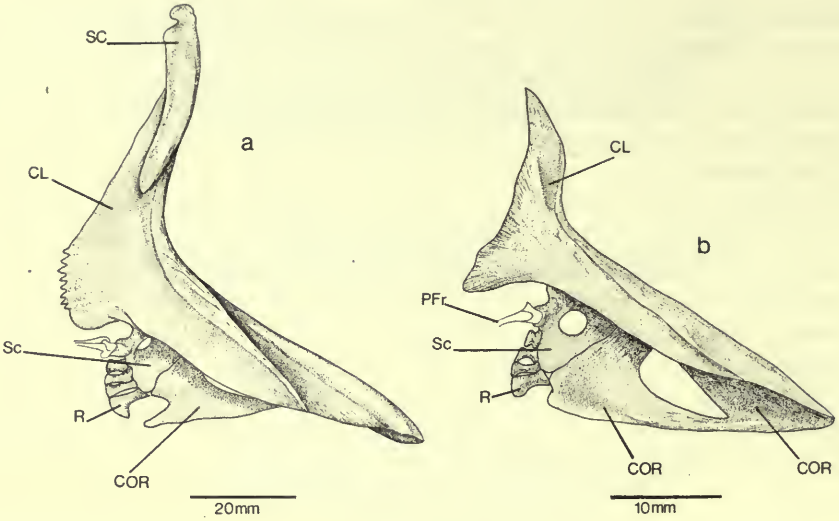


FIG. 22. Pectoral girdle (right half) in : (a) *Lates calcarifer*, (b) *L. stappersi*. (The supracleithrum is removed from this specimen.)

available skeleton of *Luciolates stappersi* the horizontal limb of the cleithrum is somewhat narrower than it is in *Lates*, and has less ventrolateral curvature ; the scapula and coracoid are also noticeably deeper in this species and the foramen enclosed between the coracoid and the medioventral margin of the cleithrum is larger (cf. Figs 22a & 22b).

The posterior angle of the cleithrum in both genera is expanded and slightly protracted, and its hind margin is serrated. These serrations are most numerous in *L. calcarifer*, *L. niloticus* and *L. angustifrons* (6–10 serrae, the uppermost often ill-defined), are fewer in *L. macrophthalmus* (5–7) and fewest (3 or 4) in *L. microlepis* and *L. mariae*. Judged on the size range of available material for any one species, the number of serrae is not obviously correlated with the fish's size, and the number may differ on either side of an individual.

In *Luciolates* the cleithral projection can have a smooth posterior border or be ornamented with from one to three weak serrations ; as in *Lates* there are lateral discrepancies in the number of serrae.

The three upper radials articulate with the scapula, and the fourth either articulates with the coracoid or partly with the coracoid and partly with the scapula.

The supracleithrum in both *Lates* and *Luciolates* is a slightly curved, dagger-shaped bone showing no interspecific variability in shape or size.

The first postcleithrum is a flat, scale-like bone, the second is elongate and spiniform (Fig. 23). No obvious interspecific or intergeneric differences were detected in either element.

The posttemporal is characterized, in both genera, by a deep and dorsally directed oval pocket formed in the body of the bone immediately lateral to the base of its

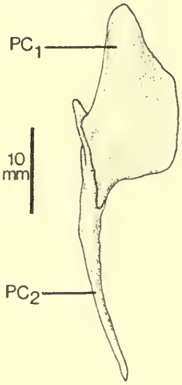


FIG. 23. *Lates calcarifer.* Postcleithra (left).

intercalar limb and a little anterior to the facet for articulation with the supracleithrum (Fig. 24). The pocket opens dorsally into the lateral line canal, and its lateral wall bulges slightly outwards ; in alizarin preparations of a young *L. niloticus* this wall has a pitted, 'strawberry-skin' appearance similar to that of the auditory bulla in many clupeomorph fishes. The pit is occupied by the distal end of the ligament which runs from the posttemporal to the *tunica externa* of the swimbladder (see p. 47 below).

Posteriorly, the shield-like body of the posttemporal is serrated, the extent and size of the serrations apparently not differing between the various species.

The extrascapula is a small Y-shaped bone, largely occupied by the lateral line sensory canals it carries (i.e. the supratemporal and temporal lines), and shows little

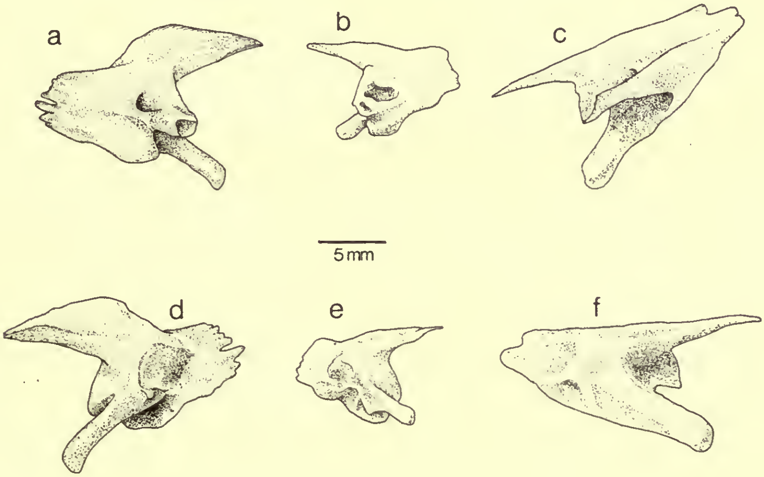


FIG. 24. Posttemporal in : (a) & (d) *Lates niloticus* (right bone), (a) lateral, (d) medial aspect. (b) & (e) *Psammoperca waigiensis* (left bone), (b) lateral, (e) medial aspect. (c) & (f) *Centropomus undecimalis* (left bone), (c) lateral, (f) medial aspect.

interspecific variability. It articulates closely with the posttemporal, the two bones together partially covering the posterior part of the posttemporal fossa.

Vertebral column (Figs 25 & 26)

The total count in all *Lates* species and in *Luciolates stappersi* is 25, viz., 11 abdominal, 13 caudal and the fused first ural and preural centra.

There are nine pairs of pleural ribs, the first pair associated with the third vertebra. On those vertebrae with parapophyses, (the eighth and subsequent abdominals have obvious parapophyses but a small projection is visible on the seventh), the ribs articulate with the posterior face of the parapophysis ; at least in *Lates* the rib articulation on the preceding centra is through a shallow facet whose ventral lip is slightly produced laterally.

The parapophyses in *Luciolates* differ from those in *Lates* in being almost vertically aligned, and by having, in all bar the first pair, a horizontal strut joining the parapophyses of each centrum near their distal tips. Also, in this genus the articulatory pit on the first three rib-bearing centra has no ventral lip, but on the fourth rib-bearing centrum (i.e. the sixth abdominal vertebra) the lip is sufficiently produced to resemble a very short parapophysis.

I have been able to check the dorsal ribs in only two species (*L. niloticus* and *Luciolates stappersi*). *Lates niloticus* has epineural ribs associated with the first

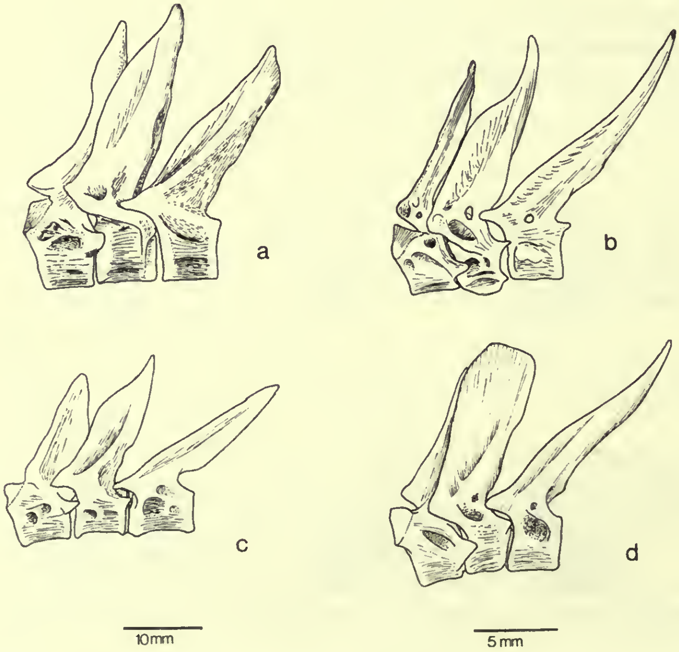


Fig. 25. First three abdominal vertebrae in : (a) *Lates angustifrons*, (b) *Psammoperca waigiensis*, (c) *L. stappersi*, (d) *Centropomus ensiferus*.

two vertebrae, and epipleurals present on the first six pairs of pleural ribs ; *Luciolates stappersi* has epineurals as in *Lates*, but the epipleurals apparently are confined to the first three pairs of ribs only.

The first three abdominal vertebrae are the most individually distinctive elements in the entire column (Fig. 25). The second vertebra is characterized by the great expansion anteroposteriorly of its neural spine, which is 2–3½ times broader than the spine of the first vertebra and about twice as broad as the spine of the third vertebra. Not only is the spine expanded but it has a characteristic outline. The anterior and posterior margins run almost parallel to one another for most of the spine's height (rather than converging with one another), and the spine narrows smoothly at a point about three-quarters of its height above the centrum. At this point, the front margin curves backwards to meet the posterior margin which may be almost vertical or, and more generally, it may have a slight posterior curvature. The hind margin of the first neural spine is closely applied to the front of the second spine, but the third neural spine slopes away from the second at a marked angle.

Neither the first nor the third neural spine has parallel margins except basally ; the margins slope towards one another over most of their height, giving the spine a narrowly triangular outline.

A variety of skeletons covering a wide size range of individuals (*c.* 16 to 1000 mm) is available only for *L. niloticus*. These skeletons indicate that the relative anteroposterior expansion of the second neural spine may at first show a positively correlated increase with increasing standard length, but that in very large fishes the spine becomes relatively narrower.

There are quite marked interspecific differences in the length–height proportions of certain centra, particularly those in the abdominal region of the column. In the descriptions that follow the first three abdominal vertebrae are excluded since those are not affected by proportional changes ; all measurements are maxima.

In *L. niloticus*, *L. macrophthalmus* and *L. longispinis*, the abdominal and caudal centra are of approximately equal length and depth or are only a little longer than deep (the latter proportions applying especially to caudal vertebrae). *Lates calcarifer* has caudal centra like those in the former species but its abdominal centra are slightly more elongate.

The abdominal centra in *L. angustifrons* have proportions similar to those in *L. calcarifer*, as do the first five or six caudal centra. Beyond that point, however, the caudal centra are noticeably more elongate (i.e. they are about 1½ times longer than deep). *Lates mariae* shows slightly greater elongation of its abdominal centra (*c.* 1⅓ times longer than deep), but the caudal centra are similar to those in *L. angustifrons*. This trend is accentuated in *L. microlepis* where, although the abdominal centra have proportions like those of *L. mariae*, the posterior caudal elements are from 1¾ to twice as long as deep ; the anterior caudals, however, are still about 1½ times longer than deep. Finally, in *Luciolates*, all the centra are clearly elongate (*c.* 1¾ to twice as long as deep) and there is no difference in proportions between the caudal and abdominal elements of the column.

There are three *predorsal bones* in all *Lates* and *Luciolates* (*pace* Fraser, 1968), the proximal end of the first lying just anterior to the first neural spine, the ends of the second and third bones lying, respectively, in front of and behind the second neural spine.

Caudal fin skeleton (Fig. 26)

There is but slight interspecific variation in the caudal skeleton of *Lates* (Fig. 26). All species have two epurals, two uroneurals and five hypurals ; the first, second and fifth hypurals are autogenous (as is the parhypural and the haemal arch and spine of the third preural centrum). The hypurapophysis is weakly to moderately developed. The neural spine on the second preural vertebra is reduced to a low crest in all species.

The principal caudal fin ray formula for all species is I,8+7,I.

Although the caudal skeleton in *Luciolates* is basically similar to that in *Lates*, it differs in having the first to fourth hypurals fused into a single plate except for a narrow proximal gap between the fused first and second, and the fused third and fourth hypurals ; the fifth hypural is free and is autogenous basally.

One small specimen (96 mm S.L.) of *Luciolates stappersi*, an alizarin preparation, has a small and free sixth hypural, the fifth hypural in this specimen being fused in with the third and fourth. Unlike the other *Luciolates* examined (by dissection and radiographically) the second and third hypurals in this fish are not apposed over their distal halves but are fused proximally instead.

As in *Lates*, there are I,8+7,I principal caudal rays in *Luciolates*.

The caudal fin margin in adult *L. calcarifer*, *L. niloticus*, *L. macrophthalmus*, *L. longispinis* and *L. angustifrons* is weakly truncate to markedly subtruncate (nearly rounded), in *L. mariae* it is truncate to weakly emarginate, but in *L. microlepis* it is so strongly emarginate as to be almost crescentic. (In juveniles, however,

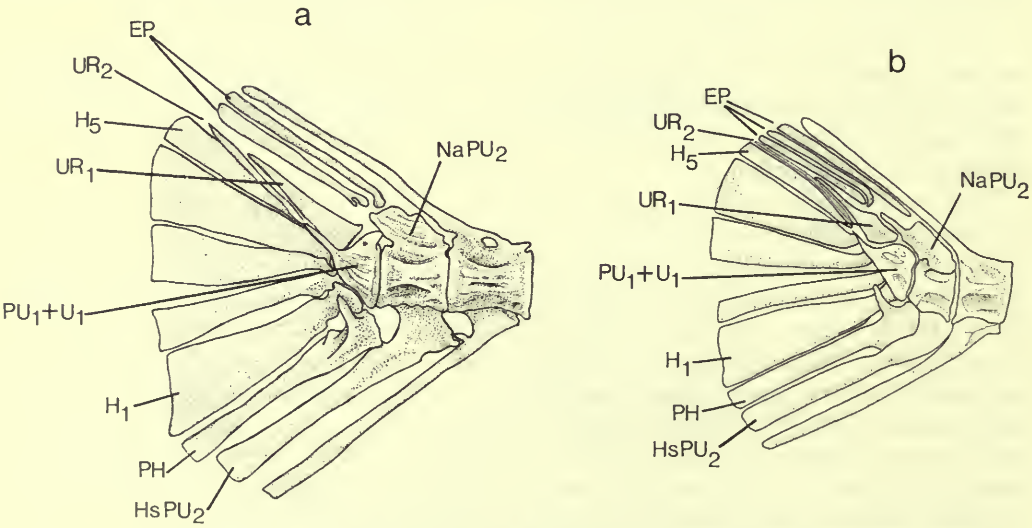


Fig. 26. Caudal fin skeleton in : (a) *Lates niloticus*, (b) *Eolates gracilis* (After Sorbini, 1973).

the margin is distinctly truncate [see Poll, 1953] or weakly subtruncate [see Boulenger, 1915].) A crescentic margin is also developed in *Luciolates stappersi*, and is deepest in fishes over 150 mm standard length.

Dorsal and anal fins

The number of pterygiophores supporting the rays of the dorsal fin (or fins) shows some slight interspecific variation; viz: *L. calcarifer* 18, *L. niloticus* 18 or 19, *L. microlepis* 19 (rarely 20), *L. macrophthalmus* 18 (rarely 19), *L. longispinis* 18 or 19, *L. angustifrons* 19 and *L. mariae* 19. Each of the first eight or nine pterygiophores carries a single spine, and no medial radials are associated with these bones. An examination of the dorsal fin ray supports in alizarin preparations of small (16–20 mm S.L.) *L. niloticus* suggests that the medial radial fuses with the proximal one (the pterygiophore) to form the elongate head of that bone. Distinct medial radials are also absent from those pterygiophores carrying the branched dorsal fin rays.

Luciolates stappersi has 19 dorsal pterygiophores, the first nine of which bear a single spine (again without the interposition of a medial radial). The seventh and eighth pterygiophores have markedly elongate heads, and each carries a short weak spine which is largely embedded in the epaxial body musculature. Superficially, these spines are well separated from each other and from the first and second dorsal fins. The ninth pterygiophore carries a longer and somewhat stouter spine which is the first ray of the second dorsal fin. Unlike *Lates*, the posterior branched rays of the dorsal fin in *Luciolates* do have distinct medial radials, even in the largest individuals examined.

The wide gap between the dorsal fins of *Luciolates* was, and in published accounts of this taxon still is, the principal diagnostic feature for the genus. It is therefore of some importance to reconsider the relative positions of the dorsal fins (or of its two sections where the fin is apparently a single unit, as in *L. niloticus*). As Poll has described (Poll, 1953) and I have been able to confirm, the Lake Tanganyika species of that genus show ontogenetically correlated changes in relative fin position. However, my observations also indicate that the definitive fin positions in these species are reached well before the cessation of obvious growth in body length.

Lates calcarifer (as compared with *L. niloticus*) has a distinctly greater interval between the last and first spines of the two fins than that existing between the penultimate and last spines of the first fin; the gap is bridged by a low membrane. In *L. niloticus* the spacing between these three rays is almost equal, and the interconnecting membrane appears to be slightly deeper. The condition in *L. macrophthalmus* and *L. longispinis* approaches that in *L. niloticus* but with a slightly greater distance between the spines in *L. macrophthalmus*.

The condition in *L. angustifrons* (the seemingly most generalized of the Tanganyika species) is either comparable with that in *L. calcarifer* or, in some individuals, the inter-fin spacing may be a little greater. Some specimens I have examined (up to 345 mm S.L.) have no membrane connecting the two fins and in a few the 'last' spine of the first dorsal is not connected with the rest of the fin; it is impossible to tell whether this latter condition is the result of damage. The smallest fish measured (90 mm S.L.) has a distinct but membrane-spanned gap between the fins.

None of the *L. microlepis* examined has a membrane connecting the fins, and in several there is an isolated spine in the gap.

The usual condition in *L. mariae* (except in fishes < 70 mm S.L.) is a distinct gap between the fins, with a single, isolated spine lying at about its midpoint. This species is unusual in having a modal dorsal spine count of nine (eight is the mode in other Tanganyika species, although occasional individuals with nine spines are recorded; see Poll, 1953).

Within the *Lates* species of Lake Tanganyika then, one finds a complete intergradation between a continuous, albeit deeply notched dorsal fin, and two separate fins with an isolated spine interposed. The condition in *Luciolates* differs from the latter state only in the greater width of the gap and the occurrence of two spines within it. *Luciolates* is, however, unusual in having only six spines in the first fin

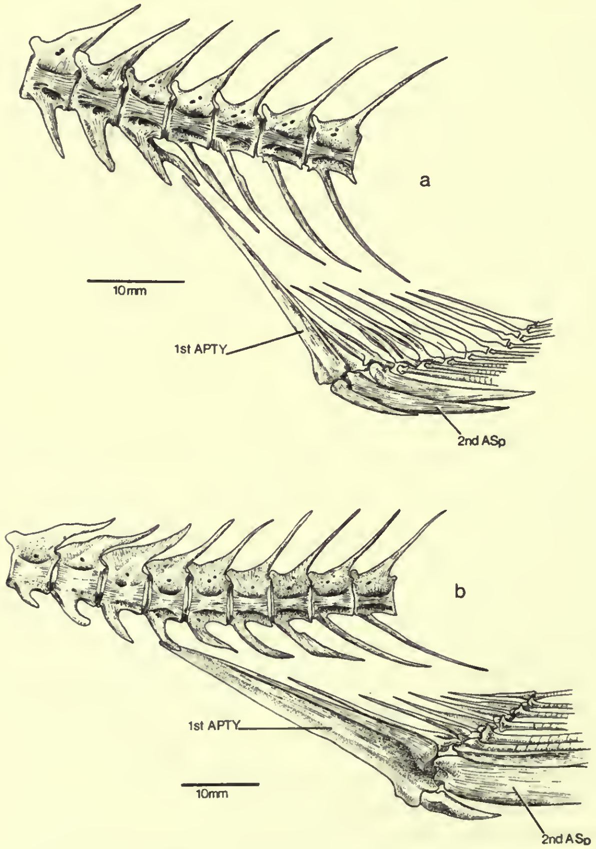


Fig. 27. First anal pterygiophore, and abdominal–caudal vertebral transition, in: (a) *Lates niloticus*, (b) *Centropomus ensiferus* (drawn from radiograph 1903.5.15:3–5 and dry skeleton 1861.12.12:13).

and one spine with only 9 or 10 branched rays in the second (compared with the usual seven spines and one spine plus 11–13, rarely 10, branched rays in the fins respectively). The two isolated spines in *Luciolates* may therefore represent the detached 'ultimate' and 'first' rays respectively of the ancestral type fin, with what we now consider to be the first spine of the second dorsal fin a neomorphic development from a branched ray. Alternatively, and as would seem more probable, the ancestral species could have had seven spines in the first dorsal fin, an isolated spine between it and the second dorsal, and the latter comprising one spine and 10 branched rays (a condition found in some specimens of *L. mariae*).

The anal fin skeleton is similar in all *Lates* species. There are nine, rarely eight, pterygiophores, the first a large double structure carrying two spines (Fig. 27a); it articulates with the cross-bar on the haemal arch of the first abdominal vertebra. All other anal pterygiophores, except the last, carry a single ray (that on the second a spinous one); the last pterygiophore carries two rays. Medial radials are absent except on the last three or four pterygiophores.

Morphologically the anal fin skeleton of *Luciolates* is like that in *Lates*, although the first pterygiophore is less robust and there are nine others in the series (i.e. a total of 10). A medial radial is present in the last four pterygiophores.

Swimbladder

One outstanding feature of the swimbladder in *Lates* and *Luciolates* is the presence of a tough connective tissue strap running from a point anterodorsally on the *tunica externa* to the posttemporal, which has a well-defined ventrolateral recess for the reception and anchorage of the strap (see above, p. 41). Katayama (1956) does not describe this connection in *L. calcarifer* but I have been able to confirm its presence in that species.

Apart from *Psammoperca* (see p. 60 below), I know of no other percoid species in which a similar swimbladder–posttemporal connection has been described, nor indeed of any connection between those two points. The functional significance of a swimbladder–posttemporal linkage is not readily apparent.

The anterior end of the swimbladder in all *Lates* species and in *Luciolates stappersi* has a deep median indentation which gives that end of the swimbladder a distinctly bilobed appearance.

Baudelot's ligament

This ligament is well defined in *Lates* and *Luciolates*, and originates from a deep pit on the basioccipital. In *L. niloticus* and *Luciolates stappersi* (the two species dissected) little or no epaxial body musculature runs below the ligament medially; laterally, however, there is a broad muscle band passing below and above it to insert partly on the anterolateral aspect of the basioccipital but mainly on the exoccipital. Thus at least the distal half of Baudelot's ligament is embedded in muscle.

The relationship of the ligament to the epaxial musculature seems to combine certain features of both the percichthyid and serranid types described by Gosline (1966), but is more akin to the serranid type.

Lateral line (Fig. 28)

In all *Lates* species the pored lateral line scales of the body continue onto the caudal fin where they extend, or almost extend, to the posterior margin of the fin. Since the posterior margin is generally abraded or damaged it is difficult to tell in the latter cases whether the absence of scales from the immediate marginal area is artefactual or not. Two other rows of pore-bearing scales are present on this fin, one lying above and the other below the median row (from which they are separated by a space usually equal to that between two fin rays). These upper and lower scale rows generally do not quite extend to the posterior fin margin. Because of their small size the scales in these rows are difficult to see in fresh and spirit-preserved specimens unless the fin is allowed to dry out completely.

Superficially there does not seem to be any linkage between the median and the other caudal lateral line scale rows ; scales in the latter rows cease to be pored at the base of the fin. Dissection of adult specimens does not reveal any deeper-lying connecting channels.

The presence of a triple lateral line on the caudal fin in *Lates* has not been recorded before, and to the best of my knowledge has not been described in any other percoid species. Since it is clearly a derived condition it is a useful indicator of the monophyletic origin of these species.

The posterior extremity of the lateral line in *Luciolates* is also triradiate, but here the three branches are interconnected by pore-bearing scales (Fig. 28b). The median row extends onto the caudal fin, but the line of pored scales is interrupted by the presence of poreless ones, and it never extends to the margin of the fin. The upper and lower lines do not extend for more than one or two scales beyond the limits of the body scales. However, in a few specimens an occasional pored scale is found some distance onto the fin membrane and in the same line as a basal branch.

Although the condition of the caudal lateral line in *Luciolates* does differ from that in *Lates* it is still a triradiate one and the two taxa can reasonably be thought to

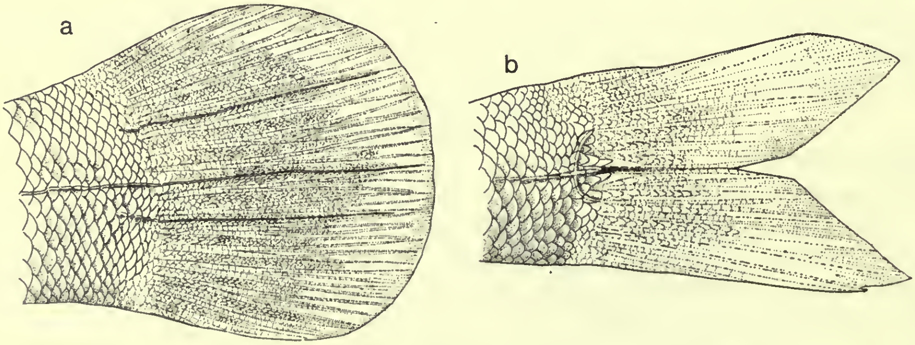


FIG. 28. Caudal fin, showing : (a) lateral line pore scales in three rows (drawn from *Lates niloticus*, but typical for all species except *L. stappersi*), (b) *L. stappersi* showing 'trident' arrangement of lateral line pore scales at body–caudal fin junction ; note that pores do not continue onto membrane of fin.

share a derived character. It is difficult to tell from the evidence available whether the *Luciolates* condition should be considered a further derivative – albeit a reductional one – of the *Lates* type, or whether it represents an early stage in the evolution of the *Lates* type.

THE INTERRELATIONSHIPS OF SPECIES WITHIN THE GENUS *LATES*, AND THE TAXONOMIC STATUS OF *LUCIOLATES* BLGR.

An analysis of the osteological and other anatomical features described in the previous sections shows that all seven *Lates* species share two derived characters, viz. (i) three rows of pored lateral line scales on the caudal fin and (ii) the ventral (i.e. horizontal) arm of the preoperculum has three or more large serrae.

There are three other derived characters (the swimbladder–posttemporal ligament, the anterior extension of the supraoccipital, and the presence of two epurals in the caudal fin skeleton), but as these are shared with *Psammoperca* (see below, p. 61) they are of no value in establishing the monophyletic origin of the genus *Lates* on the basis of synapomorph characters occurring within its constituent species. Since, however, the first two apomorph features noted above do not occur in any other members of the Centropomidae except *Lates* species, they argue strongly for the monophyly of the genus.

It is possible to subdivide the genus *Lates* by grouping together three species sharing one clear-cut apomorphy and at least four apomorph trends. Such a subdivision would bring together *L. angustifrons*, *L. mariae* and *L. microlepis*, species with an elongate ethmovomerine region in which the posterior face of the lateral ethmoid slopes backwards at a pronounced angle and the dorsolateral aspects of that bone slope sharply downwards ; this characteristic appearance of the snout region is clearly seen in Figs 5, 6 & 7. The apomorph trends shared by these species are an elongation of the caudal and posterior abdominal vertebrae (most marked in *L. mariae* and *L. microlepis* ; see p. 43), a division of the dorsal fin into two separate parts (reduced interconnecting membrane in *L. microlepis*, actual separation of the fins in *L. mariae* ; see p. 45), reduction of the pterosphenoid pedicle and internal jugular bridge (slight reduction in *L. angustifrons*, progressively greater reduction in *L. microlepis* and *L. mariae* ; see pp. 20–27) and, lastly, an elongation and narrowing of the entire skull (a trend not necessarily correlated with the former which is also manifest in species with broad skulls, e.g. *L. macrophthalmus* ; see pp. 17–19). Finally, and no doubt of significance, it may be noted that the three species are all endemic to Lake Tanganyika.

In view of these characteristics, especially the changes in lateral ethmoid morphology, it would seem phyletically proper to recognize the species as more closely related to one another than to any other *Lates* species still extant. This topic will be taken up again later (p. 51).

It is difficult to establish any well-founded scheme of interrelationships for the remaining species, *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis*. Part of this difficulty stems from the problematical relationships of *L. longispinis* and *L. macrophthalmus*, as was discussed above, p. 13. These two species alone in the group show and share definite apomorph characters* (enlarged eyes and long dorsal fin spines ; for a discussion of the reduced pterosphenoid pedicle see p. 25). All four species otherwise exhibit only the synapomorph features of the genus, and are distinguished from each other by slight meristic and morphometric differences.

The taxonomic status of *Luciolates* has never been reviewed critically since Boulenger (1914) first differentiated the genus from *Lates* on the grounds of its having ' . . . corps plus allongé, nageoires dorsales largement séparées l'une de l'autre, et ventrales insérées en arrière de la base des pectorals'.

It will be recalled (p. 47) that the condition of the dorsal fin in *Luciolates* represents a slight exaggeration of that existing in *L. mariae.* In turn, the *L. mariae* fin condition is a development of that in *L. microlepis* which is a further slight deviation from the condition found in the basic *L. calcarifer–L. niloticus* type. In other words, the apparently characteristic dorsal fin of *Luciolates* is in fact linked by intermediates with that of the most generalized *Lates* species.

Amongst the various *Lates* species similar intermediate character states can be found for most of the features which, at first sight, might seem to distinguish *Luciolates* from a generalized *Lates* species. As examples of these 'distinguishing' features one can cite the relative elongation of the vertebral centra, the protraction of the snout (especially the ethmovomerine skull region) and the general elongation and narrowing of the neurocranium. But, all are features shared with the *Lates* species of Lake Tanganyika, especially the peculiarly shaped ethmoid (cf. Figs 8, with 5–7). Even the supposedly distinctive position of the pelvic fins in *Luciolates* is closely approached by *L. mariae.*

There are, of course, certain characters in which *Luciolates* does differ trenchantly from all *Lates* species, and these features must be given particular attention.

No *Lates* species has enlarged caniniform teeth such as occur, in small numbers, near the symphysis of the upper jaw in *Luciolates* (see p. 35), none shows such a high degree of hypural fusion (see p. 44), and *Luciolates* is unique in having the three caudal extensions of the lateral line restricted to the proximal part of the fin and visibly interconnected with each other.

One may, I think, rate the dentition and fused hypural plates of *Luciolates* as derived characters. The condition of the lateral line may be primitive or it could be a secondary reduction of the *Lates* type (i.e. a derived character), although the interconnection of the lines might argue against such a conclusion. But, even if all these character states are derived ones, they are autapomorphies ; on the basis of synapomorphies *Luciolates* still has as its nearest relatives the three *Lates* species of Lake Tanganyika. Furthermore, *Luciolates* shares with these species one apomorph character (the morphology of the lateral ethmoid) which distinguishes the group as a whole from all other African species of *Lates*, as well as from the Indo-Pacific marine species *L. calcarifer.*

For these reasons I propose that *Luciolates* should be united with its nearest relatives in the genus *Lates.* At the same time I propose placing the Lake Tanganyika

---

* On the evidence currently available, *L. macrophthalmus* (from Lake Albert) and *L. longispinis* (from Lake Rudolf) could either be sister taxa derived from a common ancestor (itself a sister species of *L. niloticus*) or each could have been derived locally, in late Pleistocene times, from the population of *L. niloticus* then inhabiting these lake basins.

Lates species, that is *L. angustifrons*, *L. microlepis*, *L. mariae* and now *Lates stappersi* in one subgenus (for which the name *Luciolates* Blgr. is available), separate from *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis* which species comprise the subgenus *Lates*. Definitions and synonymies for these taxa are given on pp. 77–78.

Interrelationships within the subgenus *Luciolates* may be delimited on the basis of vertebral morphometry, the division of the dorsal fin, the morphology of the lateral ethmoid, and on neurocranial anatomy and morphology (see relevant sections on pp. 14–45).

Lates angustifrons is clearly the plesiomorph sister species of all others in the subgenus. *Lates mariae* and *L. microlepis* show generally similar degrees of specialization in all the characters noted above, and can thus be considered sister species ; since in some features (e.g. the lateral ethmoid) *L. microlepis* is less specialized than *L. mariae* it can be considered the plesiomorph member of the pair.

The greatest level of specialization is seen in *Lates stappersi* which is therefore ranked as the apomorph sister species of *L. mariae* and *L. microlepis* combined (see Fig. 37).

The difficulties of ranking species within the nominate subgenus have been discussed above (see pp. 49–50). Indeed, it is not even possible to show that this subgenus is monophyletic since its 'diagnostic' features are those plesiomorphic for the genus as a whole.

A REVIEW OF THE GENUS *PSAMMOPERCA* RICHARDSON

Introduction

There are no published accounts of the osteology and anatomy of *Psammoperca*. A brief outline of the osteology of *P. waigiensis* (Cuv.) is given here, together with some notes on various aspects of the soft anatomy in this species, particularly those features which have some bearing on the phyletic relationship of the taxon.

Fishes of the genus *Psammoperca* (Richardson, 1844) occur in coastal waters from the Bay of Bengal, the Indo-Australian archipelago, northern Australia, the Philippines and the China Sea. To a considerable extent, this distribution overlaps that of *Lates calcarifer* (see above, p. 12 ; also Fig. 36, and Weber & de Beaufort, 1929). Two nominal species, *P. waigiensis* (Cuv.) and *P. macroptera* Günth. are recognized, the latter restricted to Australia and known only from the holotype. The material I have examined is entirely of *P. waigiensis*, but the individual variability represented in these samples certainly indicates that *P. macroptera* should be considered a synonym. The question could be solved if large samples from the type locality and other regions of Australia were examined.

Superficially, *P. waigiensis* is much like *L. calcarifer* (Fig. 1), but is distinguished by its widely separated nostrils, smooth lower border to the preoperculum and to the lachrymal, and by the more extensive squamation of the dorsal and anal fins.

Osteology and anatomy of *Psammoperca waigiensis*

Neurocranium (Figs 29a–b)

The proportions and general appearance of the neurocranium closely resemble those of *Lates macrophthalmus* (cf. Figs 29 & 4b) ; that is to say, a member of the subgenus *Lates* in which there is a reduction in the length of the precommissural neurocranium without elongation of the ethmoid skull region.

The ethmovomerine region is exactly like that in members of the subgenus *Lates* ; the posterior wall of the lateral ethmoid is slightly concave and rises steeply to meet

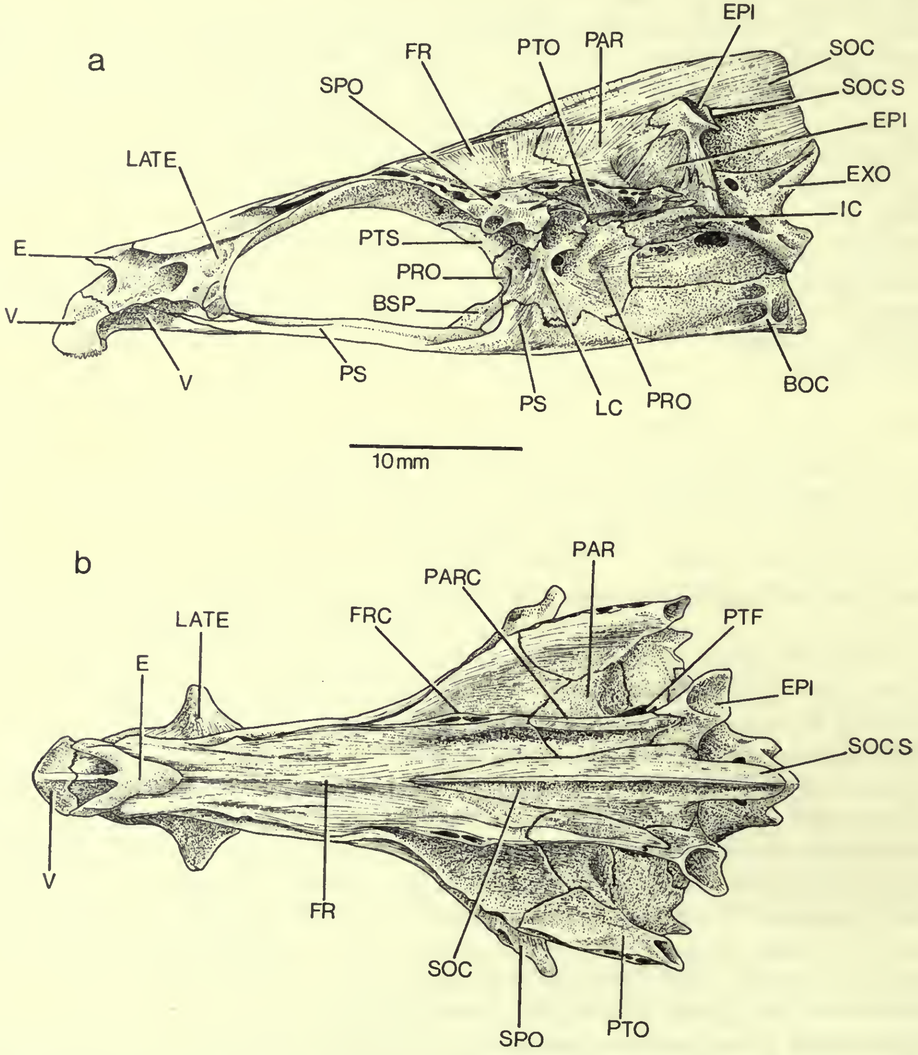

a
EPI
FR
PTO
PAR
SOC
SPO
SOC S
EPI
LATE
EXO
IC
E
PTS
PRO
BSP
V
V
PS
PS
LC
PRO
BOC
10 mm
b
PAR
PARC
FRC
LATE
PTF
E
EPI
SOC S
V
FR
SOC
SPO
PTO

FIG. 29. *Psammoperca waigiensis.* Neurocranium in : (a) left lateral view, (b) dorsal view.

the frontal, and there are two palatine and one lachrymal articulatory facets on this face. A slight intergeneric difference lies in the strongly concave posterior margin of the vomer, which gives the tooth patch in *Psammoperca* a distinct arrowhead outline in ventral view.

The precommissural region (see p. 20) of the braincase in *Psammoperca* differs in certain details from that in *L. macrophthalmus*. The pterosphenoid is about the same relative size and the ascending limb of the parasphenoid meets the prootic to create a generally similar appearance for this region of the skull. However, in *Psammoperca* there is no trace of a pterosphenoid pedicle and there is no bridge, not even a ligamentous one, across the internal jugular vein and its associated nerves (see pp. 20–26 above). In this respect the skull of *Psammoperca* resembles, most closely, that of *Lates* (*Luciolates*) *stappersi*.

The otic skull region in *Psammoperca* is like that in *Lates* (*Lates*) *macrophthalmus* as far as the relative sizes and relationships of the constituent bones are concerned, but the posterior half of the prootic is noticeably inflated and is thinner in *Psammoperca*.

The posttemporal fossa, like that in all extant *Lates* species, is large and deep, and does not have a complete bony floor. The exoccipital facets meet medially.

The autosphenotic does not extend far into the orbit medially or dorsolaterally; again the resemblance is more to *L. macrophthalmus* than to other members of the subgenus *Lates*, and there is some resemblance to species of the subgenus *Luciolates*.

The dorsocranium is, in all respects save one, like that in *L. macrophthalmus*, with the supraoccipital extending forwards to separate the frontals, high frontoparietal crests, deep excavations between these crests and the supraoccipital, and a clearly demarcated lateral shelf on the supraoccipital where the crest extends posteriorly beyond the epioccipitals. The one difference I can detect is the absence of a bone-enclosed supraorbital transverse commissure in *Psammoperca*. The cephalic lateral line system in other respects, however, is like that in *Lates*.

The parasphenoid resembles closely that in *Lates* but is more sharply angled upwards from the level of the ascending limb; in this respect *Psammoperca* resembles species of the subgenus *Luciolates*.

Hyopalatine arch and the preoperculum (Fig. 30)

Again, it is only in certain details that the hyopalatine arch of *Psammoperca* differs from that arch in *Lates*.

Psammoperca has no tooth patch on the ectopterygoid, and the dermopalatine tooth patch is very narrow. According to Weber & de Beaufort (1929), ectopterygoid teeth are present in *P. waigiensis* but I have been unable to detect any on the specimens I have examined. Ectopterygoid teeth are absent in some specimens of *Lates* (*Luciolates*) *stappersi*, and it is interesting to recall that the dermopalatine tooth patch is narrowed to an extent comparable with that in *Psammoperca*. The palatine in *P. waigiensis* has a distinct dorsal ridge on the autopalatine immediately in front of the facet for articulation with the lateral ethmoid. This ridge is absent in all members of the subgenus *Luciolates* and is but weakly developed in species of the nominate subgenus.

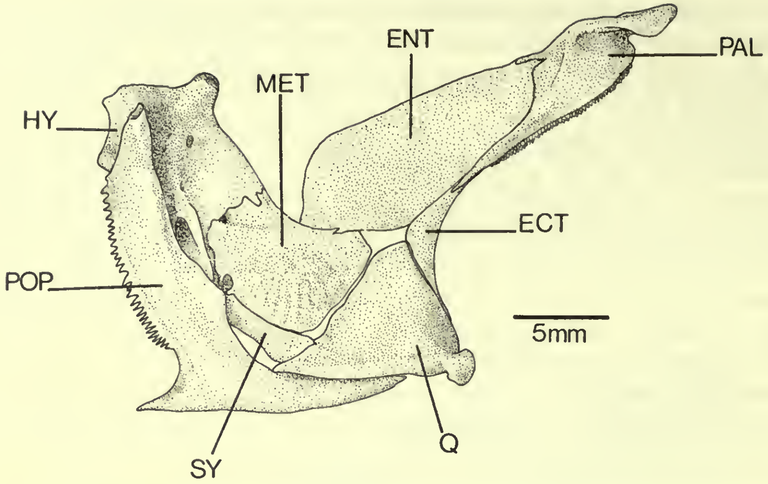


FIG. 30. *Psammoperca waigiensis*. Hyopalatine arch, including preoperculum (right side), viewed laterally.

As in *Lates*, the vertical limb of the preoperculum has a finely serrated posterior border, and the mandibular–preopercular sensory canal is bone enclosed (but opening through three ventrally directed and elongate pores on the horizontal arm). The margin of the ventral limb, however, is entirely smooth except for a stout, posteriorly directed spine at the angle between the vertical and horizontal limbs (Fig. 30). A similar spine is, of course, present in all *Lates* species but *Psammoperca* lacks the three or four stout and ventrally orientated spines on the horizontal limb. *Lates* (*Luciolates*) *stappersi*, it will be recalled (p. 30), often shows some reduction in the size of these spines, but in no individual are they entirely wanting.

Circumorbital bones (Fig. 31)

The five circumorbital bones are very similar to those in *Lates*; the relative elongation of the lachrymal and of the fifth circumorbital in *Psammoperca* is more like that seen in members of the subgenus *Luciolates*.

The lateral line canal is bone enclosed but opens to the exterior through five pores on the lachrymal, a pore between each articulation of the individual bones, and a ventral pore on the third circumorbital bone.

The suborbital shelf (on the third bone) is well developed to an extent almost equalling that found in members of the subgenus *Lates*; it extends dorsally to about the upper end of the fourth circumorbital bone.

The most marked difference between the circumorbital series in *Psammoperca* and *Lates* lies in the completely smooth ventral margin to the lachrymal and second circumorbital bones. These bones are strongly serrated in all *Lates* species, except *L. stappersi*, but even in that species some definite trace of the serrations does remain on the posterior part of the lachrymal (see p. 32 and Fig. 13c–d).

Opercular series (Fig. 14c)

The operculum of *Psammoperca*, like that in *Lates*, is armed with a single stout spine developed at the posterior end of the stay running from the articular facet for the hyomandibular boss. Indeed, the entire opercular series is like that of *Lates*, the relatively elongate interoperculum having the proportions of that bone in *L.* (*Luciolates*) *mariae*, *L.* (*Luciolates*) *microlepis* and *L.* (*Luciolates*) *stappersi* rather than that in other species of the genus. As in *Lates*, the sub- and interopercular bones of *Psammoperca* are thin.

Jaws (Figs 32a–c)

The maxilla, supramaxilla and premaxilla are, except for the coarser teeth on the latter bone, identical with those elements in species of the subgenus *Lates*.

The bones of the lower jaw (dentary, anguloarticular and retroarticular) are also like their counterparts in members of that subgenus ; again, the teeth are stouter than in *Lates*.

Branchial skeleton

In its basic morphology and in the details of its upper pharyngeal dentition the gill arch skeleton of *Psammoperca* is identical with that of *Lates niloticus* (see p. 35). The only difference I can detect from the one *Psammoperca* skeleton studied is that the regularly arranged, small, rectangular tooth plates lying laterally on the gill arch above the filaments (the supralamellar plates, see p. 37) are restricted to the outer side of the first four gill arches (in *Lates* plates are present on both aspects of an arch).

This reduction in tooth plates should be considered as a derived condition since a marked reduction or even the complete loss of free dermal tooth plates is a feature of the more specialized percomorph groups.

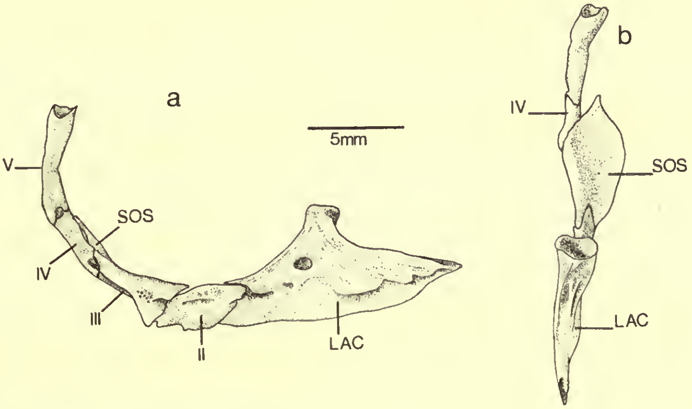


FIG. 31. *Psammoperca waigiensis*. Circumorbital bones (right) in : (a) lateral view, (b) viewed dorsally and somewhat anteriorly.

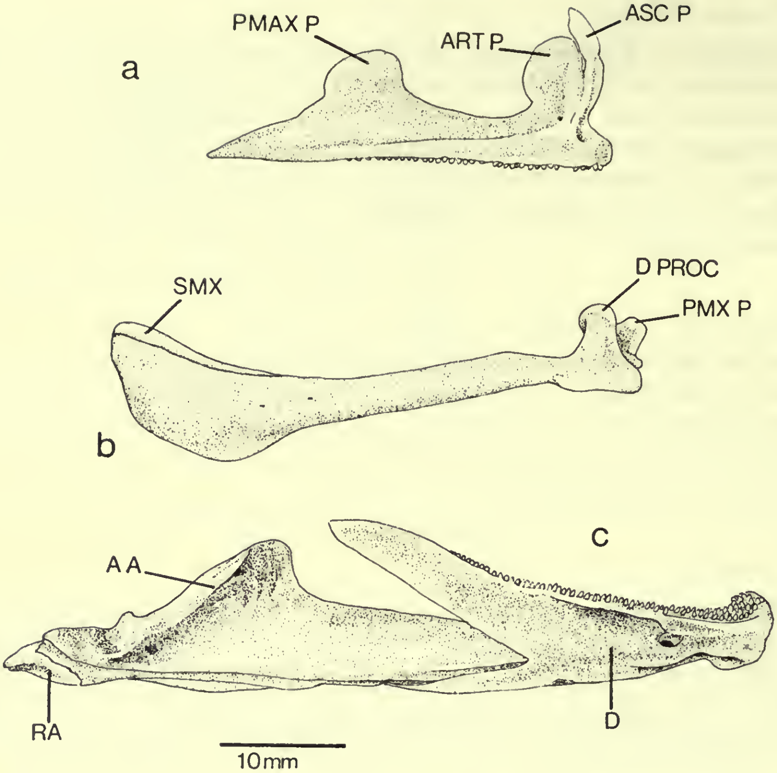


FIG. 32. *Psammoperca waigiensis.* (a) Premaxilla (right) in lateral view. (b) Maxilla (right) in a slightly oblique dorsal view to show supramaxilla. (c) Dentary (right), with anguloarticular and retroarticular, in lateral view.

Hyoid arch skeleton (Fig. 33)

The only marked difference between the hyoid skeletons of *Psammoperca* and *Lates* (especially members of the subgenus *Lates*) is the presence in the former of a moderately large, ovoid tooth-patch firmly attached to the broadly spatulate basihyal.

Psammoperca has seven branchiostegals, the posterior two of which articulate laterally with the epihyal, the next two with the ventrolateral face of the ceratohyal, and the first three with the ventral margin of that bone.

The presence of a basihyal tooth plate must be considered a plesiomorph character for the genus, the only living member of the Centropomidae in which it has persisted.

Pectoral girdle and associated bones (Fig. 34)

The one obvious difference between the pectoral girdles (i.e. supracleithrum, cleithrum, scapula and coracoid) of *Psammoperca* and *Lates* is the absence of serrations on the posterolateral angle of the cleithrum. In all other respects the girdles

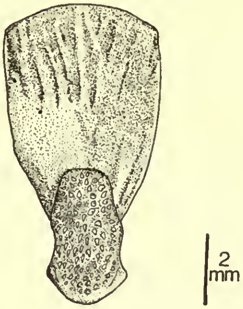


FIG. 33. *Psammoperca waigiensis.* Dorsal view of basihyal, showing tooth plate.

in the two genera are similar, but with a greater resemblance in overall proportions between the girdle of *Psammoperca* and that in the subgenus *Lates.*

Although in *Psammoperca* there are no serrations at the posterior cleithral angle, the bone in that region is drawn out into a short but well-demarcated spine.

As in *Lates,* the three upper fin radials articulate with the scapula, and the lowest with the coracoid.

There are two postcleithra, but in *Psammoperca* the upper member of the pair is less expansive than in *Lates.*

The posttemporal and extrascapula are similar in both genera, the posttemporal in *Psammoperca* even having the same kind of pit for the reception of the swimbladder ligament (see p. 41), but it does lack serrations on its hind margin.

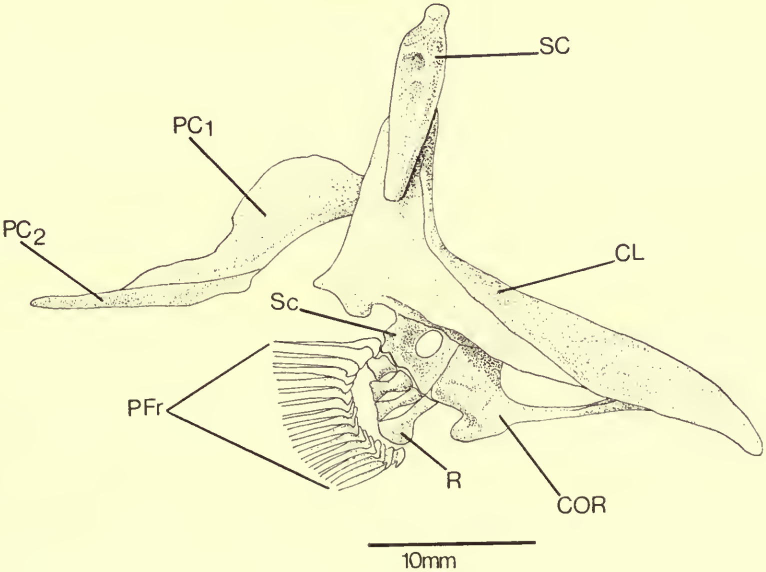


FIG. 34. *Psammoperca waigiensis.* Pectoral girdle (right half) with supracleithrum *in situ* and post-cleithra displaced posterodorsally. Lateral view.

Vertebral column

The total vertebral count in *P. waigiensis* is 25, comprising 11 abdominal vertebrae, 13 caudal, and the fused first preural and ural elements of the caudal fin skeleton.

There are nine pairs of pleural ribs, the first pair carried on the third vertebra, the last pair on the eleventh abdominal vertebra ; this latter pair of ribs, instead of sloping gently backwards parallel with the preceding pair (as in *Lates*), runs almost horizontally and generally overlaps the proximal tip of the first anal pterygiophore.

The first definite parapophyses appear on the seventh vertebra, and are but a little shorter than those on the succeeding centra, although there is a slight and posteriorly progressive elongation of these processes. Anterior to the seventh vertebra, the ribs articulate with a shallow pit on the centrum. Where parapophyses are present, the rib articulates with the posterior face of the process.

In all these features, except for the better developed first and second parapophyses, and the angling of the last pair of ribs, *Psammoperca* is like *Lates* (see p. 42).

Epineural ribs are present on the first three vertebrae, and epipleural ribs on at least the first four pleural ribs. (These data were obtained from radiographs.)

The first three vertebrae are shown in Fig. 25b ; their close resemblance to those in *Lates* is obvious (cf. Fig. 25a). One slight difference is in the development of a low median ridge on the ventral face of the second centrum of *Psammoperca*.

As in *Lates*, the neural spine of the second vertebra is much broader than the spine of the first and third centra, has its anterior and posterior margins parallel over much of their lengths, and tapers rather abruptly to form a slightly hooked tip. The angle between the posterior face of the second spine and the anterior face of the third spine is from 20° to 25°.

Except in the first four vertebrae, all centra are a little longer than deep, the relative length of the centrum increasing somewhat in the posterior abdominal vertebrae, which have about the same proportions as the caudal vertebrae. In this respect the centra in *Psammoperca* are rather more like those in *Lates* (*Luciolates*) *angustifrons* than in other species of that subgenus or in species of the nominate subgenus.

There are three *predorsal bones*, the first lying immediately anterior to the first neural spine, the second and third situated immediately before and behind the tip of the second neural spine.

Caudal fin skeleton (Fig. 35)

The caudal skeleton in *Psammoperca* differs from that in *Lates* in one important respect, namely the presence of a single uroneural (see p. 44). Otherwise there is great intergeneric similarity in this structure (viz. 2 epurals, 5 hypurals, I,8+7,I principal fin rays and a low neural crest on the second preural vertebra [lower, in fact, than in *Lates*]).

There is, as far as can be detected from radiographs, probably no fusion between any of the hypurals, although in one fish (240 mm S.L.) of the eight examined, hypurals 3 and 4 are so closely apposed as to appear fused. The first and fifth hypurals are autogenous, the others are fused to the underlying vertebral support.

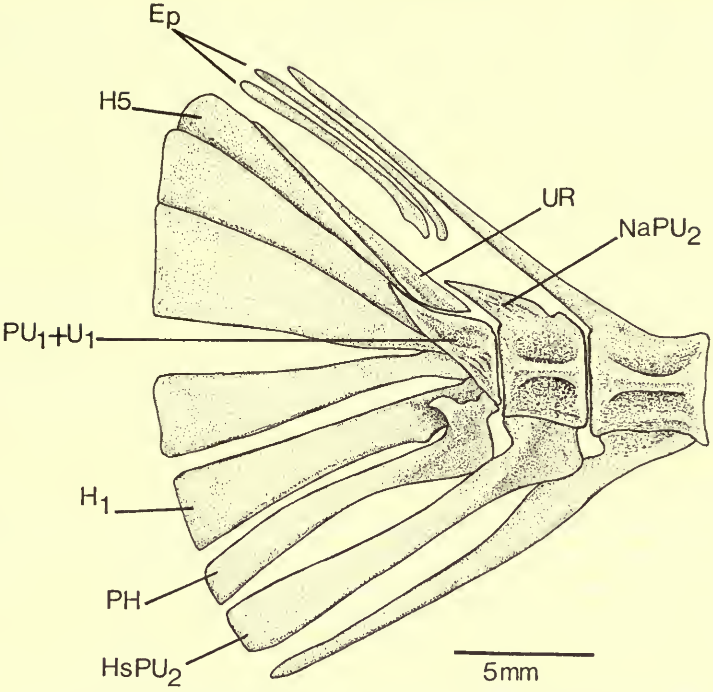


FIG. 35. *Psammoperca waigiensis.* Caudal fin skeleton (drawn from specimen 1872.9.2:10–11).

The posterior margin of the caudal fin is rounded.

A single uroneural must be considered a derived feature, and in this respect the caudal fin skeleton in *Psammoperca* is, relative to that in *Lates*, more specialized. Indeed, since there are in *Psammoperca* two and not three epurals the caudal fin skeleton is more specialized than that in any member of the Serranidae (where there are, invariably, three epurals – but one uroneural – in the fin skeleton ; see Gosline, 1966).

Dorsal, anal and pelvic fins

There are 19 pterygiophores (proximal radials) in the dorsal fin skeleton, each one except the last supporting a single fin ray. Although an occasional member of the subgenus *Lates* may have 19 pterygiophores (see p. 45), the usual number in that taxon is 18. Nineteen, however, is the modal number of pterygiophores (20 the unusual one) in species of the subgenus *Luciolates*.

Unlike *Lates*, *Psammoperca* has some of the dorsal fin spines (the fifth through the eighth) associated with discrete medial radials ; a medial radial is also associated with the last branched ray in this fin. *Lates* (*Luciolates*) *stappersi* alone amongst the *Lates* species has medial radials (associated with the posterior four or five branched rays).

The dorsal fin is deeply indented to form an anterior part with seven spines, and a posterior portion with one spine and 12 branched rays. A continuous but low membrane connects the two parts of the fin. The spacing between the spines of the two fin divisions is fairly even (cf. *Lates* species, p. 45).

The anal fin skeleton comprises nine pterygiophores, of which the first is a double structure and carries two spines. All other pterygiophores, except the last, carry a single spine or ray. (Total fin ray count III,8.) Medial radials are absent from all pterygiophores except the last. (In *Lates* species medial radials are present on the last three or four pterygiophores, see p. 47.)

The first of the nine anal pterygiophores, like that in *Lates*, is a stout and elongate bone and is in contact proximally with the haemal spine of the first abdominal vertebra.

The origin of the pelvic fins lies slightly behind that of the pectoral fins ; in other words the fins have the same positions as in *Lates* (*Luciolates*) *stappersi*.

Swimbladder

As in *Lates*, so in *Psammoperca* there is on each side of the swimbladder anteriorly a tough connective tissue strap extending from the *tunica externa* to the posttemporal. The position, shape and size of the strap are identical in both genera (as are the modifications to the posttemporal, see pp. 41 and 47).

The gross morphology of the swimbladder resembles that in *Lates*. The *tunica externa* is thick, and a pair of short blunt processes extends forward on either side of a median invagination of the swimbladder. *Psammoperca* does differ, however, in having a narrow posterior diverticulum extending outside the visceral cavity. In a single specimen dissected, this caudal swimbladder prolongation lay on the left side of the first anal pterygiophore ; it is embedded in the body musculature of that region and does not penetrate into the haemal arches of any caudal vertebrae.

Baudelot's ligament

The ligament is well developed and its relationships with the body musculature in the cervical region are like those described for *Lates niloticus* on p. 47 ; that is, it closely approximates to the serranid type described by Gosline (1966).

Lateral line

Unlike *Lates* there is only one series of pore-bearing scales on the caudal fin of *Psammoperca*. These small scales are an uninterrupted continuation of the body lateral line scales ; they extend almost to the posterior margin of the caudal fin. In one of the nine specimens available, a few widely separated pore scales were found on the fin membrane between a pair of rays on the lower part of the fin.

THE RELATIONSHIPS OF *PSAMMOPERCA*

The close overall resemblance between *Psammoperca* and *Lates* has long been recognized (Regan, 1913), and has even resulted in a false record of *Psammoperca* for the Japanese fauna (see Katayama, 1956).

A detailed examination of the characters shared by the two taxa shows that many must be ranked as primitive features (i.e. symplesiomorphies) and therefore of little value in estimating relationships. Included amongst the symplesiomorphies are the vertebral count, the presence of a single opercular spine, similarities in gill arch anatomy and dentition, the single spine carried on the first pterygiophore of the dorsal fin, and many details in syncranial morphology and anatomy.

There are, however, four derived characters shared by *Psammoperca* and *Lates* which are not present in any other members of the Centropomidae. These synapomorphies are :

(i) A swimbladder–posttemporal ligament (and correlated modifications to the posttemporal bone) ; see p. 60.
(ii) A large spine at the posterior angle of the preoperculum.
(iii) Two epurals in the caudal fin skeleton ; see p. 58.
(iv) An anteriorly extended supraoccipital which separates the posterior parts of the frontals.

On the basis of these characters it is reasonable to conclude that *Lates* and *Psammoperca* are members of the same lineage, a lineage distinct from that of *Centropomus* (see below, p. 62). To indicate this relationship I propose placing *Psammoperca* and *Lates* together in one subfamily, the Latinae. Members of the genus *Centropomus* would thus constitute a second subfamily, the Centropominae, which can be readily defined on the basis of several specialized characters (see p. 67 below).

Psammoperca waigiensis (and, where these features can be checked, also *P. macroptera* ; see p. 51 above) differs from all or most species of the genus *Lates* in at least 14 features. In the list that follows, the condition of these features in *Lates* is given in parentheses.

1. A single series of lateral line scales on the caudal fin. (Three series.)
2. A single uroneural. (Two uroneurals.)
3. Some spine-bearing dorsal fin pterygiophores with a median radial. (None.)
4. No tooth patch on the ectopterygoid. (Present, but reduced in *L. stappersi*.)
5. No spines on the ventral (horizontal) limb of the preoperculum. (Three or four spines.)
6. Ventral margin of the first infraorbital bone (lachrymal) smooth. (Serrated, strongly so in most species.)
7. No pterosphenoid pedicle or internal jugular bridge. (Pterosphenoid pedicle present in all species except *L. stappersi* and *L. mariae* ; internal jugular bridge present in all species, even if reduced to a ligament.)
8. Transverse commissure of supraorbital lateral line system absent or poorly developed. (Present and well developed.)
9. Dermal tooth patch fused with basihyal. (Absent.)
10. Supralamellar tooth plates (p. 37) present only on the outer side of each gill arch. (Present on both sides.)
11. Posterior margin of the posttemporal smooth. (Serrated.)
12. A single short spine at the posterior angle of the cleithrum. (One large and two smaller spines.)
13. Posterior extravisceral extension of the swimbladder. (None.)
14. Second dorsal and anal fin entirely covered by small but densely arranged scales. (Squamation restricted to about the proximal two-thirds of the fin.)

In some of these characters (e.g. 1, 3, 5 and 9) *Psammoperca* is more primitive than any *Lates* species ; in others (2, 4, 7, 10 and 13) it shows derived characters. The status of characters 6, 11, 12 and 14 is at present indeterminable. (See discussion on pp. 30–32.)

It is on the basis of the unique derived characters (i.e. autapomorphies) found in each of the two taxa that I would maintain them as distinct genera, the implication being that *Psammoperca* split off from the common latine lineage before the evolution of a serrated preoperculum and the tripartite lateral line extension onto the caudal fin. The derived characters seen in *Psammoperca* (especially the loss of a pterosphenoid pedicle, the presence of a single uroneural, the loss of certain branchial arch tooth plates, and the loss of ectopterygoid teeth) must have evolved after this split occurred. In these features *Psammoperca* is certainly more 'advanced' than is *Lates*.

It is interesting to note that a reduction and ultimate loss of the pterosphenoid pedicle is seen in certain *Lates* species of the subgenus *Luciolates* (see pp. 20–27), and that *Lates* (*Luciolates*) *stappersi* also shows a considerable reduction in, and occasionally the loss of, ectopterygoid teeth. Furthermore, this species also shows a marked weakening of the serrations on the lachrymal. Similar parallel trends in all three characters are found amongst the species of *Centropomus* (see below) thus suggesting that this is the manifestation of a potentiality possessed by the common ancestor of all living centropomids.

THE RELATIONSHIPS OF *CENTROPOMUS* WITH THE LATINAE

Fraser (1968) has given a good account of the osteology of five species of *Centropomus* but he was unable, through lack of published information, to compare fully these species with members of the genera *Lates* and *Psammoperca*. He did, however, list a number of differences between *Lates* and *Centropomus* and these will be commented upon below.

In my comparison of *Centropomus* and the Latinae I have drawn on Fraser's (op. cit.) information and supplemented it from dissection, radiographs and dry skeletons of *C. parallelus* Poey, *C. pectinatus* Poey, *C. armatus** Gill, *C. unionensis** Bocourt, *C. robalito** Jordan & Gilbert, *C. nigrescens** Günther, *C. ensiferus* Poey and *C. undecimalis* (Bloch) ; species not described by Fraser (op. cit.) are marked with an asterisk.

The *neurocranium* in all *Centropomus* species is narrow and elongate, with a pronounced relative lengthening of the ethmovomerine region. In these respects it resembles the neurocranium of *Lates* (*Luciolates*) *mariae* and *L.* (*Luciolates*) *stappersi*, but it does differ in having only a gently angled parasphenoid (or even a straight one ; cf. *C. pectinatus*, text-fig. 4, and *C. undecimalis*, text-fig. 5, in Fraser (1968), with Figs 7 & 8 above), and in having the postotic region of the skull relatively longer.

Within the *Centropomus* species I have examined, there is a trend of neurocranial elongation which closely parallels that found in members of the *Lates* subgenus *Luciolates*.

Another parallelism with *Lates* is seen in the reduction of the pterosphenoid pedicle and internal jugular bridge.

The pedicle and bridge are best developed in *C. ensiferus* (see text-fig. 6 in Fraser, 1968) where the condition of the bridge is like that in *L.* (*Luciolates*) *angustifrons* (see p. 24 and Fig. 5a). A noticeable difference, however, is that, in *C. ensiferus*, there is no ascending arm of the parasphenoid and the bridge is formed by contact between the pterosphenoid and prootic. (The prootic in all *Centropomus* contributes to the posteroventral margin of the orbit ; in *Lates* this rarely happens because part of the ascending parasphenoid arm usually rises in front of the prootic. This tongue of parasphenoid is, however, very narrow in the more specialized species of the subgenus *Luciolates*.)

In all other *Centropomus* species I have examined or which are figured by Fraser (1968), excepting *C. undecimalis*, the pterosphenoid pedicle is either reduced (e.g. *C. pectinatus*) or is greatly reduced to a small bony knob (that is, to conditions comparable with those in very small *L.* (*Lates*) *niloticus* or those in adult *L.* (*Luciolates*) *microlepis* ; see p. 26). In *C. undecimalis* there is no trace of a pterosphenoid pedicle ; in other words a situation directly comparable with that in *L.* (*Luciolates*) *stappersi* and in *Psammoperca waigiensis*.

Correlated with this reduction in the pedicle, the internal jugular bridge is reduced from a narrow bony strut in *C. ensiferus* to a ligament in the other species (except *C. undecimalis*), again paralleling exactly the trend seen in *Lates* (pp. 21–26). In *C. undecimalis* even the ligament has disappeared (at least in the specimen of 175 mm S.L. I dissected) ; this, it will be recalled, is the condition also found in *Psammoperca* (p. 53).

Probably as a correlate of the lengthening ethmoid-vomerine skull region, the shaft of the vomer in all *Centropomus* species is much broader anteriorly and has a closer sutural union with the lateral ethmoid than it does in any latine species. In other details, however, this region of the skull is generally similar in both *Centropomus* and the Latinae.

The otic region in *Centropomus* is bullate, more markedly so in some species than in others, but always more inflated than in any *Lates* species and rather more so than in *Psammoperca*.

An outstanding inter-subfamilial difference is found in the lateral line system of the dorsicranium. In *Lates* and in *Psammoperca* all three major canals are bone enclosed. In *Centropomus* the canals are in the form of laterally orientated open gutters, with only the posterior part of the supraorbital line completely tubular. The frontal cross-commissure is also open (with the gutter directed medially), as is the entire length of the frontoparietal branch (whose gutter is directed laterally).

Fraser (1968) has corrected Regan's (1913) erroneous observation that parietal crests are absent in *Centropomus*, but as compared with *Psammoperca* and *Lates*, the parietal crests, and their counterparts on the frontals, are low and very poorly defined, and do not extend to the posterior margin of each parietal (often being confined to the anterior half of that bone).

The supraoccipital in *Centropomus* does not extend so far anteriorly as it does in *Lates* and *Psammoperca*, its tip barely separating the frontals and only reaching a level with a vertical through the middle or the posterior third of the prootic.

There are few noteworthy differences in the *hyopalatine* arches of *Centropomus* and the Latinae. As Fraser (1968) noted (*pace* Regan, 1913), ectopterygoid teeth are present in *Centropomus*. From Fraser's drawing (op. cit., text-fig. 11) one gains the impression that a metapterygoidal lamina is present in at least some *Centropomus* species, but I cannot confirm this from the dry skeletons I have examined.

There are several inter-subfamilial differences in the morphology of the *preoperculum.* First, the lateral line canal in *Centropomus* is an open gutter, the opening orientated posteriorly on the vertical limb of the bone and ventrally on its horizontal limb. It is the upper rim of this gutter that has been described as a 'ridge' on the preoperculum in *Centropomus* species (see Fraser, 1968). In the Latinae, where the canal is bone enclosed and tubular no 'ridge' is, of course, detectable.

A second and pronounced difference is in the ornamentation of the preoperculum, a difference most obvious when *Centropomus* is compared with *Lates.* In *Centropomus,* as in *Lates* and *Psammoperca,* the posterior margin of the vertical limb is serrated (less regularly so in *Centropomus*), but the horizontal limb in that genus has a number of low, rather irregular serrations that are enlarged posteriorly at the angle of the bone. In no *Centropomus* species is there any indication of the three (or four) large triangular spines that characterize all *Lates* species ; likewise, no *Centropomus* has the completely smooth horizontal preopercular arm of *Psammoperca.* Also, unlike both *Lates* and *Psammoperca,* there is no single, stout spine at the posterior angle between the two preopercular arms ; instead, in *Centropomus* there are a variable number of spines, all of which are somewhat larger than those preceding and succeeding them on the arms of the bone, but none is as large nor as distinctive as the single spine of the latines.

The *operculum* in *Centropomus* lacks a spine at its posterodorsal angle (see p. 55) but otherwise the opercular series shows no marked departure from its counterpart in the Latinae.

The open lateral line gutters of the *circumorbital bones,* the reduced serration of the ventral lachrymal border, and the relatively short fourth and fifth circumorbitals are the most obvious inter-subfamilial differences noted in this region of the skull. Apparently the subocular shelf in *Centropomus* is like that in *Psammoperca* and members of the latine subgenus *Lates,* but I have been unable to check this point in all *Centropomus* species, and in particular those with narrower and more elongate heads.

Apart from some slight proportional differences, the major feature differentiating *jaw* elements in the two subfamilies is the much shorter ascending process of the premaxilla in *Centropomus.* In the Latinae the ascending process is at least one and a half times the height of the maxillary process (see p. 34) but in *Centropomus* the two processes are of equal height (cf. text-fig. 12 in Fraser, 1968, with Figs 15, 16 & 32 above).

The basic *gill arch* morphology and dentition are similar in *Centropomus* and the Latinae, although the tooth plates associated with the basibranchials are slightly more elongate in at least some members of the Centropominae. The supralamellar tooth plates in most *Centropomus* species which I have dissected (*C. ensiferus, C. parallelus, C. pectinatus, C. undecimalis* and *C. armatus*) show a unique arrangement not found in any member of the Latinae. The plates are present only on the outer aspect of the second to fourth gill arches, and are fused, in pairs, with the bases of the gill rakers on that aspect of the arch; occasionally a single plate may occur between a pair of gill rakers. An exception is provided by a small (160 mm S.L.) specimen of *C. parallelus* in which the plates are serially arranged like those in *Psammoperca.*

A slightly larger fish (220 mm S.L.) shows a condition intermediate between that in the smaller specimen and that of the other species (and specimens of *C. parallelus*) I examined. Possibly this change in plate arrangement is a growth phenomenon.

All *Centropomus* species have 24 *vertebrae* (including the fused first ural and preural centra), comprising 9 abdominal and 15 caudal elements. (Fraser, 1968, gives a count of 10 + 14, indicating that we differ in our interpretation of which vertebra constitutes the first caudal element; I identify it as that vertebra with which the first anal pterygiophore articulates.) All members of the Latinae, in contrast, have 25 vertebrae (11 abdominal and 14 caudal elements).

There are seven or eight pairs of pleural ribs in centropomines (nine in the Latinae), the number apparently showing some intraspecific variability. The first rib articulates directly with the third vertebra. Definite parapophyses are developed on the seventh abdominal centrum but a low process occurs on the sixth vertebra. Anterior to these centra the ribs articulate as in the Latinae, that is, with a pit in the centrum. Also as in the Latinae, the ribs articulate with the posterior face of the parapophysis when these are present.

As far as I can tell from radiographs, the shape and proportions of the centra in all *Centropomus* species are like those in *Lates calcarifer.* That is, posterior to the third vertebra all the centra are slightly longer than deep, with little difference in proportion between abdominal and caudal elements. Apart from the neural spine on the second vertebra the first three vertebrae are like their counterparts in latine fishes. The second vertebra, however, has a very greatly expanded neural spine (see Fig. 25d) into the anterior face of which the entire posterior margin of the first neural spine is fitted. Fraser (1968) has shown that the proportions of the second neural spine change with age in at least some species of *Centropomus*; the spine in young fishes resembles that in adult *Lates* and *Psammoperca* (see Fraser, op. cit., text-fig. 14, and pp. 454–5; and cf. Figs 25a–c above).

All *Centropomus* species have three *predorsal bones*, the first situated above the tip of the first neural spine, the second at about the middle of the expanded second spine, and the third lying immediately behind that spine. Fraser (1968) states that there are only two predorsals in *Lates*, but this is not so (see p. 43 above); there are, in fact, no intergeneric differences in this feature.

A distinct gap separates the two *dorsal fins* in all *Centropomus* species; the size of the gap, however, shows some specific variation. Unlike those Latinae with separate dorsals (members of the subgenus *Luciolates*; see p. 45), the centropomines have no isolated spines between the fins. The head of the seventh pterygiophore is drawn out posteriorly so that it effectively underlies the gap between the fins; the spine which this pterygiophore carries thus becomes the first (and only) spine of the second dorsal fin.

There are 16 or 17 dorsal pterygiophores in *Centropomus* (cf. 18 or 19, rarely 20 in the Latinae), none of which, as far as I can determine, has a separate medial radial (see p. 45). The first dorsal pterygiophore, unlike that of the latines, carries two spines ; except for the last dorsal and first anal pterygiophores, all the others carry a single spine or ray.

The dorsal fin ray counts in *Centropomus* are VII or VIII and I,8 or 9 (cf. VI–VIII and I,10–13 in all Latinae except *Lates* (*Luciolates*) *stappersi* which has VI+I+I and I,9 or 10). Thus in the centropomines there has been not only a trend towards separation of the dorsal fins (a trend also apparent in the latines, see p. 46 above) but also a reductional trend in the number of dorsal fin rays, particularly the branched rays. Interestingly, if the two independent and much reduced fin spines are 'removed' from the fin formula of *Lates* (*Luciolates*) *stappersi*, the result – save for an extra branched ray – is the formula of a *Centropomus* (i.e. VI+I+I and I,10 ⟶ VI and I,10).

A most characteristic feature of all *Centropomus*, and one not even approached by any member of the Latinae, is the very strong and long first *anal pterygiophore* (see Fig. 27b) ; in many species there is also hypertrophy of the second anal spine. Despite the length of this pterygiophore it extends only a little further distally (i.e. towards the vertebral column) than does its counterpart in the Latinae. The greater length of the bone in *Centropomus* is accommodated by the bone sloping obliquely backwards so that the articulation for the spines lies in a vertical below about the seventh rather than the second or third abdominal vertebra as is the case in *Lates* (Fig. 27a) and *Psammoperca*.

The *caudal fin skeleton* in *Centropomus* differs from that in the Latinae in either one (*Lates*) or two (*Psammoperca*) characters and is of a more primitive kind. Primitive features in *Centropomus* are the three epurals (two in Latinae) and the two uroneurals. *Lates* also has two uroneurals but only one is present in *Psammoperca* (the fin skeleton in that genus being the most evolved within the Centropomidae).

All *Centropomus* species have a deeply forked caudal fin whereas in the Latinae the fin is usually rounded or truncate, although it is weakly forked in some species of the *Lates* subgenus *Luciolates*. Like the Latinae, the caudal fin formula of the Centropominae is I,8+7,I.

The *pectoral girdle* and fin skeleton are basically alike in the Centropominae and Latinae except for slight differences in the postcleithral elements.

The *posttemporal* in *Centropomus* lacks the cavity and associated bullation that characterize this bone in *Lates* and *Psammoperca*, a consequence of there being no swimbladder–posttemporal ligament in *Centropomus* (see below). Otherwise the posttemporal is similar in both subfamilies. The extrascapula in *Centropomus* is also basically like that in the Latinae, but it is characterized by having the lateral line canals situated in open gutters and not enclosed in bony tubes (see p. 41 above).

In those *Centropomus* species which I have been able to dissect, the anterior end of the *swimbladder* has no medial invagination (see p. 60 above). However, in some species there are a pair of short horns arising from the dorsolateral aspect of the bladder and extending part way towards the skull ; in none could I find any direct connection between the skull and the horns, and neither could I find any trace of a swimbladder–posttemporal ligament such as occurs in all members of the Latinae. The development of the swimbladder horns seems to be restricted to certain species.

When present these appendages may be short, simple and anteriorly directed, or, as in *C. undecimalis*, they may be elongate and curved backwards to lie laterally along the swimbladder (see Meek & Hildebrand, 1925). This latter condition is reminiscent of that found in certain species of Sciaenidae (a family in which there is also an extension of the lateral line onto and reaching the margin of the caudal fin ; the possibility of there being some phyletic relationship between sciaenids and centropomids is under review).

Baudelot's ligament is present in *Centropomus* and is moderately well developed. The relationships between this ligament and the body muscles are like those in the Latinae (see p. 60 above), with little or no muscle passing medially below the ligament, but with a broad band passing underneath it laterally to insert on the basioccipital and exoccipital.

A single extension of the body *lateral line* scale series onto the caudal fin is found in all species of *Centropomus* (there are three extensions in *Lates* but only one in *Psammoperca*). In *Centropomus*, as in the Latinae, the caudal extension of the lateral line is continuous to the margin of the fin or almost so.

When all these characters are taken into account, it is clear that the Centropominae (i.e. *Centropomus* species) differ from the Latinae (*Lates* and *Psammoperca* species) in a number of features. Some of these differences involve the retention of characters primitive for the family whilst others represent the development of unique specializations shared only by *Centropomus* species. In the former (i.e. plesiomorph) category may be listed the caudal fin skeleton, the short supraoccipital bone, the single lateral line extension onto the caudal fin, and the absence of a swimbladder–posttemporal ligament. The autapomorphic features of the Centropominae are more numerous and include the open cephalic lateral line canals, the separation of the dorsal fin, the hypertrophy of the first anal pterygiophore (and at least relative hypertrophy of the second anal spine), the absence of medial radials throughout the dorsal and anal fins, the development of a curved and posteriorly protracted head on the seventh pterygiophore of the dorsal fin (see p. 65), the development in most species of anterior horns on the swimbladder, the incorporation of the supralamellar tooth plates into the gill rakers, and the elongation of the skull, especially its ethmovomerine region (with which feature may be correlated changes in the shape of the ethmoid and vomer).

There are other differences, like the absence of an opercular spine, the forked caudal fin, and the markedly reduced squamation of the dorsal, caudal and anal fins, whose apo- or plesiomorph status is uncertain.

On the basis of those characters that are clearly synapomorphic the *Centropomus* species can be recognized as a monophyletic group and one which, although sharing a common ancestry with the Latinae, is clearly distinct from that lineage. It is for this reason that I propose giving the *Centropomus* species-group coordinate ranking (as the subfamily Centropominae) with the Latinae (see also above p. 61 ; and p. 75 below for diagnoses).

When the mosaics of apo- and plesiomorph characters within the two subfamilies are compared it becomes impossible to decide which taxon should be considered the plesiomorph sister group of the other. However, it does seem that what we are now observing is the product of vicariant differentiation from a once widespread basic centropomid taxon, a differentiation that produced the Centropominae in America, and the Latinae in Asia and the Mediterranean region (including Africa), leaving each group with its own association of primitive and derived features.

Fraser (1968) noted certain shared characters amongst the various species of *Centropomus*, and from their pattern of occurrence concluded that three phyletic lineages are represented amongst the living species. Unfortunately, Fraser does not give a really critical analysis of the characters on which his phylogeny is constructed and it is thus impossible to test the supposed interrelationships of the three lineages he hypothesizes. In particular it would seem that his monotypic lineage comprising *C. pectinatus* is more likely a member of the *C. ensiferus* – *C. robalito* lineage, and not, as is expressed in Fraser's diagram, one distinct from the other two lineages and occupying an equal phyletic relationship with both of them (see Fraser, 1968, text-fig. 9).

Although Fraser's analysis is not documented in terms of synapomorph and symplesiomorph characters it obviously shows that similar trends can be found within the Centropominae and the Latinae. This aspect is particularly well demonstrated in the neurocranial morphology and in the reduction of the pterosphenoid pedicle and internal jugular bridge. There is also inter-subfamilial similarity in the trend towards greater separation of the two parts of the dorsal fin. In this trend the Latinae appear not to have evolved much beyond the early phases, whereas the centropomines have carried the trend further and no longer preserve traces of its earlier stages within their numbers.

FOSSIL CENTROPOMIDAE

Apart from identifications based solely on otoliths,* all species of fossil centropomids so far discovered are currently referred either to *Lates* or to *Eolates* Sorbini (see Sorbini, 1973), that is, to the subfamily Latinae.

The time range of these fossil taxa extends from the Eocene to the Holocene, and their geographical range from the Paris Basin, through Austria, Portugal, northern Italy and Croatia to Egypt, the Sahara and eastern Africa (Sorbini, 1973; Greenwood, 1974; Greenwood & Howes, 1975).

With the exception of some material from Europe (Sorbini, 1973) the majority of fossils are from Africa and are in the form of disarticulated and damaged bones. The problems of specific (or, indeed, generic) identification when dealing with material of this nature need not be stressed. In most instances the fossil bones have been compared with their counterparts in *Lates calcarifer* and *L. niloticus*. If the fossils are from Africa, and the bones are not noticeably different from their counterparts in *L. niloticus* the material was either referred to that species or, and probably more accurately since diagnostic features are rarely preserved, merely to *Lates* sp.

---

* *Psammoperca sheppeyensis* Frost 1934, *Centropomus superpendens* Frost, 1934 and *C. excavatus* Stinton, 1966, all from the London Clay (Eocene), are species described from otoliths only. Since so little is known about otolith morphology in living centropomids and because no skeletal material is available for the species, these records can at present contribute little to our understanding of centropomid phylogeny and biogeography.

When obvious morphological differences could be detected the remains have been taken to represent different species (e.g. *L. fajumensis* Weiler, 1929; *L. karungae* Greenwood, 1951; *L. rhachirhinchus* Greenwood & Howes, 1975).

Because these species are based on fragmentary, disarticulated bones it is impossible to determine their phyletic relationships with each other or with the extant species of Latinae (see discussions on *L. rhachirhinchus* in Greenwood & Howes, 1975). About all that can be said with any certainty is that latine centropomids had, by late Miocene times, a distribution that included Egypt, Tunisia and eastern Africa (Lakes Victoria and Albert regions) and that at least one species, *L. rhachirhinchus*, showed several derived characters even when compared with extant species of that genus (Greenwood & Howes, 1975). All these remarks are, of course, based on the assumption that the taxa are correctly placed in the genus *Lates*; in no case is it possible to check on the autapomorph characters used here to define the genus (see p. 77), the generic identity being based on an overall similarity between the fossil bones and their counterparts in extant *Lates* species.

The situation is little better for the three European species in which the entire skeleton is preserved, viz. *L. partschii* Heckel, 1855 (Miocene, Vienna Basin); *L. croaticus* Kramberger, 1902 (Miocene, Croatia) and *L. macropterus* Bassani, 1899 (Oligocene of Vicenza).

I have not been able to examine any material of *L. croaticus*, and the only published description and figures of this species are inadequate for critical interpretation, although Kramberger (1902) does give a vertebral count of 27, that is two more vertebrae than in any other member of the Latinae for which the count is available. The status and relationships of this nominal species must therefore remain *incertae sedis*.

Sorbini (1973) has re-examined *L. macropterus*, but was unable to draw any definite conclusions about its relationships. Again it is impossible to check on any diagnostic characters of phyletic importance.

Lates partschii (Miocene of Vienna) has been thoroughly redescribed by Sorbini (1973), who also published a photograph of the holotype, and a close-up picture of its caudal skeleton. But once again certain critical details are either not preserved, are obscured, or are damaged. For instance, there seems to be only a single and median row of lateral line scales on the caudal fin but one cannot be certain that dorsal and ventral scale rows were not present. There are certainly only two epurals in the caudal fin skeleton, and there are, apparently, two uroneurals, both features which are characteristic of *Lates* (see pp. 44 and 77). From this and other circumstantial evidence given in Sorbini's account, it seems likely that *partschii* can be placed in *Lates*, but it is impossible to determine its relationships with any extant species of that genus.

Fortunately, many important features are preserved in the extensive material of *Eolates* that is available for study (Sorbini, 1973; personal observations on specimens in the collections of the British Museum (Natural History))*.

---

* Two nominal species are recognized, *Eolates gracilis* (Agassiz) 1833, and *E. macrurus* (Agassiz) 1833. According to Sorbini (1973), *E. macrurus* may yet prove to be a synonym of *E. gracilis*. For this reason, and because the osteology of *E. gracilis* is much better known, only that species is taken into account in the discussions that follow.

Eolates gracilis is distinguished from all *Lates* species by at least one character complex (the caudal fin skeleton), and probably by two other characters as well (the absence of upper and lower lateral line scale rows on the caudal fin, and the disposition of the branchiostegal rays).

I have examined eight specimens of *E. gracilis* (from the BMNH collections) in which the caudal fin is well preserved. In all, the median lateral line scale row is clearly developed and it is also possible to see other scales, often still in their rows, on other parts of the fin. None of these other scales is perforated and I am confident that only one lateral line scale row (the median one) is preserved. My colleague, Dr K. Banister, has recently examined *E. gracilis* holotype in the Paris Museum and reports that only a median row can be detected in this specimen as well.

The caudal fin skeleton in *E. gracilis* (Fig. 26b) shows a well-developed neural spine on the second preural centrum (spine greatly reduced in *Lates*), three epurals (two in *Lates*) and two uroneurals (two uroneurals also present in *Lates*). In other words, the caudal fin skeleton is of a more primitive type than that in *Lates*. (It will be recalled that *Centropomus* also has three epurals, but the second preural arch and spine are reduced and resemble those in *Lates*.)

A possible third intergeneric difference concerns the number and disposition of the branchiostegal rays, but this requires confirmation since it is based on data available from only one of the *E. gracilis* specimens examined by Sorbini (1973). In the sole specimen from which a branchiostegal ray count could be made Sorbini (op. cit.) records, with some uncertainty, a total of eight rays (seven in *Lates* and other centropomids). Judging from the photograph of this specimen (Sorbini, 1973, Plate IV, fig. 1), I should doubt that the fragment at the anterior end of the ceratohyal is indeed part of a branchiostegal ray.

There is, however, no doubt that in this specimen all the branchiostegal rays are associated with the ceratohyal. According to McAllister (1968) this condition is not found in any living percoid fish ; there is always at least a half articulation between a ray and the epihyal. The rays in the *E. gracilis* specimen are in no way disarranged, and the posterior one is well forward of the epi-ceratohyal junction. Clearly no decision can be made on the validity of this apparent intergeneric difference (or its apparent uniqueness amongst percoids) until further specimens can be examined.

Like the preoperculum in *Lates* this bone in *Eolates* has three large ventral spines on its horizontal limb, and an enlarged spine at the posterior angle of the bone. Also as in *Lates*, there is a single, large spine on the posterodorsal margin of the operculum in *Eolates*. Ornamentation of the cleithrum and on the first infraorbital bone (lachrymal) is similar in *Eolates* and *Lates*, but the phylogenetic importance of these latter characters is probably not great.

Regrettably, little detailed information can be obtained about the morphology of the neurocranium in *Eolates*. Sorbini (1973) gives no description of the posterior orbital region of the skull, presumably because in his material, as in that of the BMNH, this area of the head is either crushed or obscured by other bones overlying it. Thus it is impossible to determine what type of pterosphenoid pedicle and internal jugular bridge is present.

The ethmoid region is generally well preserved, and resembles that found in members of the subgenus *Lates* (see p. 19 above).

In a few *E. gracilis* specimens the posttemporal is well preserved; it seems to show the slightly bullate outer surface that, in living centropomids, is associated with the insertion point of a swimbladder–posttemporal ligament (see p. 41 above), a derived feature characterizing members of the subfamily Latinae (see above, p. 66).

In brief, *Eolates* (as represented by *E. gracilis*) is clearly a member of the subfamily Latinae and shares at least one derived character (the ventral preopercular spines) with the genus *Lates* (see p. 31). *Eolates* differs from *Lates* in having only one series of lateral line scales on the caudal fin (presumed in this context to be a primitive feature, see p. 48 above), and in having a caudal fin skeleton that is primitive in relation to this skeleton in *Lates* (see above, p. 66). A third intergeneric difference is in the less deeply indented dorsal fin of *Eolates*, a feature with which may be correlated the equal spacing between the 'last' (i.e. shortest) spine of the anterior part of the fin and the longer 'first' spine of the fin's posterior half. This character too should be considered a plesiomorph one because a deeply divided fin is a basal condition in the centropomid trend leading towards completely separate first and second dorsal fins (see above, pp. 46 and 65).

All the features discussed so far indicate that *Eolates* should be considered more primitive than *Lates*. In phyletic terms it should be ranked as the plesiomorph sister group of that taxon. The relationship of *Eolates* within the subfamily Latinae is, therefore, best indicated by uniting *Eolates* with *Lates* in a single tribe (Latini, new tribe) which would then become the sister taxon of the tribe containing only the genus *Psammoperca* (tribe Psammopercini nov.).

Sorbini (1973) also recognizes the affinity of *Lates* and *Eolates*, but he would regard the relationship as an ancestor–descendant one (op. cit.: 41) rather than that of recent shared common ancestry as is proposed here.

Sorbini's claim that '... The living marine species *L. calcarifer* presents the greatest relationship to fossil Tertiary species, which lived in a similar habitat' (Sorbini, 1973: 41) certainly cannot be substantiated by the meristic and morphological data available from these fossils. For example, as interspecific similarities between *L. calcarifer* and *E. gracilis* Sorbini lists (op. cit.: 36) '... disposizione delle vertebre, n. raggi branchiostegi, habitat ...'. The habitat is similar, but what importance can be attached to this feature in a family with several euryhaline species? The arrangement of the vertebrae in *Eolates* is like that in several *Lates* species, while the reference to the number of branchiostegal rays is, I presume, a *lapsus* for 'spine branchiali'. *Eolates* has either seven or eight branchiostegal rays (there are seven in all other centropomids; see above, p. 70), but nine gill rakers (the same number as *L. calcarifer*). However, a low gill raker count (8–12) is common to several *Lates* species, and is apparently the primitive state for the family as a whole.

BIOGEOGRAPHY

The contemporary world distribution of the Centropomidae (Fig. 36) strongly suggests a Tethyan distribution for the common ancestor of its two subfamilies, the

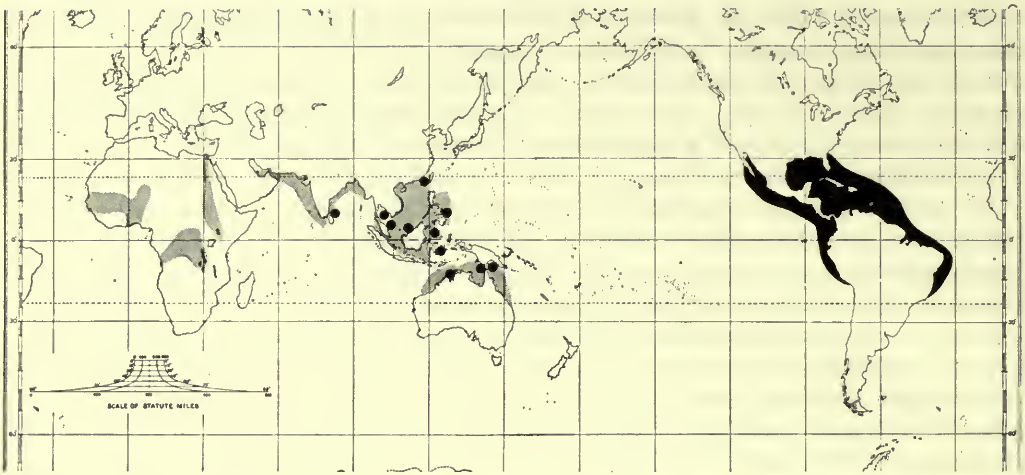


FIG. 36. World distribution of extant species of Centropomidae. Stippled areas: *Lates* species (outside Africa = *L. calcarifer*). Black spots: *Psammoperca* species (probably only one, *P. waigiensis*). Black area; *Centropomus* species.

Centropominae (America) and the Latinae (Mediterranean, African freshwaters and Asia).

The Centropominae, on this hypothesis, have evolved in the tropical New World, probably in estuarine and marine habitats, and the Latinae principally in African freshwater habitats. There is, however, a major dichotomy in the Latinae, between the tribes Latini and Psammopercini, which must have taken place before the Latini invaded Africa.

As evidenced by various European fossil species (see above, pp. 68–71, and Sorbini, 1973) and by the wide dispersal of *Lates calcarifer* (see p. 12), the Latini were and still are successful coastal fishes. The greater diversification of the tribe in African freshwaters can probably be attributed to the greater opportunities for speciation provided by the developing tropical lakes and river systems of later Tertiary and Quaternary Africa. (For a summary of these historical factors see Beadle, 1974.) It will be recalled that there are seven extant and at least three extinct *Lates* species in Africa, compared with the single extant (*L. calcarifer*) and three extinct marine or estuarine species (see above, p. 69; also Sorbini, 1973; Greenwood, 1974; Greenwood & Howes, 1975).

There are, of course, at least nine species of *Centropomus* (Centropominae) all of which are essentially marine species (although some freely enter freshwater; Meek & Hildebrand, 1925). Trans-isthmian isolation could account for four of these species (Fraser, 1968) but there still remain the other five species to contrast with the single marine *Lates* species (*L. calcarifer*) of the Indo-Pacific region. The causal factors involved in this aspect of *Centropomus* speciation are not apparent.

It is interesting to compare the morphological radiation undergone by the Centropominae and Latinae, and to notice the marked parallelism apparent in the two groups. For example, in both subfamilies there are trends of specialization leading to the reduction and loss of the pterosphenoid pedicle and internal jugular bridge (p. 63), to elongation of the skull through differential lengthening of the ethmoid region (p. 62), to an increase in the number of gill rakers on the first gill arch, to a reduction in the number of supralamellar tooth plates (p. 64), and towards the division and then separation of a primitively continuous dorsal fin (see p. 66). So similar are all the features involved in any one of these trends that one can eliminate any possibility of convergence. The similarities must reflect shared genotypic factors stemming from common ancestry.

The absence of *Lates* (or some related latine fish) from the present-day Mediterranean Sea may, as Sorbini (1973 : 40) suggests, be due to climatic changes adversely affecting the one or more species that were present in the Mediterranean basin during parts of the Tertiary (Sorbini, op. cit., especially text-fig. 10). Increasing salinity in the developing Mediterranean may also have had its effect on local populations.

During the Eocene and Miocene, species of *Lates* were also present in Africa (Sorbini, 1973 ; Greenwood, 1974). The Eocene fishes from the Fayum in Egypt may have been estuarine and marine (Weiler, 1929), as may have been the Miocene species from Tunisia (Greenwood, 1973). However, Miocene records of *Lates* from the equatorial regions of Lake Victoria (Greenwood, 1951) and Lake Albert (Greenwood & Howes, 1975) show that some latine species had adjusted fully to freshwater environments, and that enough time had elapsed since the first invasion for latine species to have reached areas some 3750 km inland from the Mediterranean coast.

Like all other fossil Latinae from Africa, the Miocene species are referred to *Lates* solely on the overall similarity between the preserved fossil bones and their counterparts in extant *Lates* species. Such critical features as the nature of the lateral line scales on the caudal fin and the morphology of the posttemporal bone are unknown for any one of them. One Miocene species, *L. karungae* Greenwood, 1951, from Rusinga Island, Lake Victoria, is represented by only a few vertebrae ; the specific diagnostic features for this taxon relate to the morphology of the third vertebra (Greenwood, 1951). The other taxon, *L. rhachirhinchus*, from the Lake Albert–Lake Edward region of Zaire is better represented by numerous skeletal parts (Greenwood & Howes, 1975). It differs from all other *Lates* species in several features, many of which can be considered as derived, and one of which (vertebral proportions) is shared with certain members of the endemic subgenus *Luciolates* from Lake Tanganyika (see p. 43 above, and Greenwood & Howes, op. cit.). Even though it is impossible to identify specifically the *Lates* remains from the Miocene and Pliocene deposits in North Africa and Egypt, *L. rhachirhinchus* is morphologically quite distinct from those taxa.

Thus, one may conclude from this situation either that more than one taxon invaded Africa or that, by Miocene times, the population of *Lates* in the Lake Albert–Lake Edward region had undergone marked morphological differentiation, presumably in isolation from its parental stock. The same arguments could be applied to *L. karungae* although in this instance there is less evidence for the extent to which the morphological differentiation had progressed.

Sorbini (1973) postulated certain time sequences and migration routes to explain the present-day distribution of *Lates* species in Africa. Basically the problem Sorbini sets out to explain is the widespread occurrence of one species, *L. niloticus*, in the Nile, Niger, Zaire, and Senegal river systems, and in Lakes Rudolf, Albert and Chad, in contrast to the occurrence of four endemic species (one supposedly a distinct genus) in Lake Tanganyika. He notes the former occurrence of *Lates* in other lakes (Edward and Victoria) but is not concerned with the factors that led to these local extinctions, and neither does he take into account the endemic species that coexist with *L. niloticus* in Lakes Rudolf and Albert.

There are two basic tenets in Sorbini's hypothesis, first that the various invasions he postulates originated in Egypt, and second that fossils identified as *L. niloticus* are indeed representatives of that species. As I have discussed above the latter assumption is not necessarily acceptable, and neither can I find any *a priori* grounds for postulating repeated and temporally extended invasions from a single area (in this argument, Egypt).

That a species of *Lates* had reached the regions of Lake Victoria and Lake Albert–Lake Edward by Miocene times is not disputed (see above), and Sorbini's argument for the contemporaneous presence of a *Lates* species in the Lake Tanganyika basin is also acceptable. Why, then, should *Lates* not have occurred in other Miocene rivers and water bodies, environmental conditions, of course, permitting such colonization? To the best of my knowledge there is no evidence to show that suitable conditions were confined to the regions from which Miocene fossils have been recovered. Thus I find it difficult to understand why, in order to explain the present distribution of *L. niloticus*, Sorbini should postulate two invasions, each following different routes, but both originating from Egypt during the Pliocene and continuing through the Pleistocene. Presumably a major reason for putting forward this hypothesis is the fact the fossils identified as *L. niloticus* are first recorded from the Pliocene of Egypt, thereby implying the origin of that species in Egypt at a later date than the one at which another species (*L. karungae*) was already present in the Lake Victoria area (and, had he known it, a second species *L. rhachirhinchus* was present in the area of Lake Albert–Lake Edward ; Greenwood & Howes, 1975).

In view of the known distribution for Miocene *Lates* and because of the uncertainties associated with the specific identification of most fossil *Lates* remains, a simpler hypothesis can be made, viz. :

At some stage prior to the late Eocene a species of *Lates* invaded Africa, possibly through more than one entry point, but almost certainly from the north. In the course of time this species gradually dispersed through the various river systems with some isolated populations evolving into distinct species now extinct (e.g. *L. rhachirhinchus* and *L. karungae*, possibly also *L. fajumensis*), and others or their descendants (like the endemic species of Lake Tanganyika) still surviving. A little modified descendant of the original invader, the species now recognized as *L. niloticus*, continued to spread (by such means as river capture or lake extension) until it came to have its present distribution. The *L. niloticus*-like fossils of Pleistocene times (Greenwood, 1959, 1974 ; Sorbini, 1973) stand witness to a much wider area for the distribution of *Lates* and even probably for the species *L. niloticus* (but of that point we must remain uncertain).

It is unnecessary here to discuss the history of *L. niloticus* in lakes such as Rudolf and Albert which may, at some time in their histories, have dried out completely, and which have had complex relationships with the River Nile and other lakes (see discussions in Greenwood, 1959, 1974; also Beadle, 1974). There is still, however, the problem of the endemic *Lates* species in the two lakes, *L. longispinis* in Lake Rudolf and *L. macrophthalmus* in Lake Albert. In brief, on morphological criteria (p. 12) these species are apparently more closely related to one another than either is to *L. niloticus*, the species from which each was supposed to have been derived at some time during the Pleistocene (Worthington, 1932; Holden, 1967). On the evidence currently available it is impossible to determine whether *L. longispinis* and *L. macrophthalmus* do in fact represent survivors of a distinct lineage or if, as Worthington (1932) postulated, they are offshoots of earlier *L. niloticus* populations that once inhabited the two lakes (see discussions on pp. 13 and 14).

DIAGNOSES FOR THE CENTROPOMIDAE, ITS SUBFAMILIES, GENERA AND SUBGENERA

CENTROPOMIDAE Poey, 1868

Poey, F., 1868, *Repertorio Fisico-Natural de Cuba*, **5**, no. 2: 280. (See also Gill, T., 1883, *Proc. U.S. natn. Mus.*, **5**: 484–485).

TYPE GENUS: *Centropomus* Lacépède, 1802.

DIAGNOSIS. Percoid fishes, some attaining a large size (up to 2 m), with the neural spine of the second vertebra markedly expanded in an anteroposterior

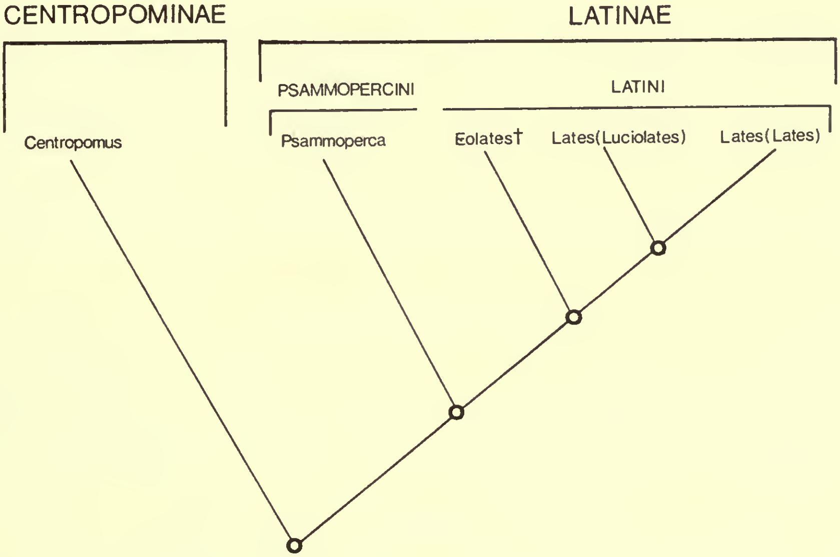


FIG. 37. Cladogram to illustrate phyletic relationships within the Centropomidae.

direction, and the pored scales of the body lateral line continued onto the caudal fin, reaching the posterior margin of that fin in all but one species. Twenty-four or 25 vertebrae (including the fused first ural and preural centra of the caudal skeleton); pleural ribs associated with parapophyses except on the first three to five rib-bearing vertebrae (the first two vertebrae of the column are without ribs); 3 predorsal bones. Dorsal fin either deeply divided, the first part entirely spinous (7 or 8 spines), the second of one spine and 8–11 branched rays, or the two parts of the fin separated by a distinct gap; anal fin with 3 spinous and 6–9 branched rays; caudal fin with 17 principal rays, its posterior margin rounded, truncate or forked. Scales ctenoid, small to moderate in size, dorsally not extending forward on to the head beyond the level of the midpoint of the eye (usually only to the level of the posterior margin of the orbit) but present on the cheek and operculum; scaly sheath at the base of the anal and soft dorsal fins, but squamation extending onto all fin membranes (including that of the caudal). No scales on the maxilla; a small supramaxilla present. Teeth on the premaxilla, dentary, vomer, palatine and, in most species, the ectopterygoid; teeth absent, except in *Psammoperca*, from the glossohyal. Jaw teeth generally small, viliform or conical, and arranged in several rows. Pterosphenoid pedicle and internal jugular bridge present in all but three or four species, although variously developed; frontoparietal crests present. Seven branchiostegal rays. Pseudobranch present. About 20 extant species from marine, estuarine and freshwater habitats in the tropical New World (Atlantic and Pacific coasts), tropical Africa (predominantly fresh- or brackish water species), and from Indo-Pacific coastal waters. Six extinct species (some from Europe), the earliest being from the Eocene of Monte Bolca.

Subfamily **CENTROPOMINAE**

Centropomid fishes with 24 vertebrae; the cephalic lateral line canals not enclosed in bony tubes but carried in skin-covered bony gutters; the supraoccipital barely separating the frontals; the first anal pterygiophore hypertrophied and inclined backwards at an oblique angle; no opercular spine but three or four enlarged spines at the posterior angle of the operculum; no swimbladder–posttemporal ligament developed; no isolated spine or spines situated between the first and second dorsal fins (these fins always separated by a distinct gap); pseudobranch superficial.

TYPE GENUS: *Centropomus* Lacépède, 1802.

A single genus *Centropomus* (type species *Sciaena undecimalis* Bloch, 1792), generic diagnosis as for the subfamily with, additionally, caudal fin skeleton having three epural and two uroneural bones. The genus is confined to the tropical waters of North, Central and South America, and occurs on both the Pacific and Atlantic coasts. A key to the species of *Centropomus* is provided by Meek & Hildebrand (1925), and supplementary information by Chávez (1961) and Rivas (1962).

Subfamily **LATINAE** Jordan (1923)

Centropomid fishes with 25 vertebrae; the cephalic lateral line enclosed in bony tubes; the supraoccipital extending far forward between the frontals; the first anal pterygiophore not hypertrophied, and inclined backwards at only a slight angle ; a single well-developed opercular spine and a single, enlarged spine at the posterior angle of the preoperculum ; a stout ligament connecting the swimbladder with the posttemporal (which is itself modified to receive the ligament) ; dorsal fin deeply indented or separated into two fins (between which there are one or two isolated spines) ; pseudobranch covered.

TYPE GENUS : *Lates* Cuvier & Valenciennes, 1828.

Three genera, two extant and one extinct.

The two extant genera are :

PSAMMOPERCA Richardson, 1844

TYPE SPECIES : *Labrax waigiensis* C. & V., 1828.

Latine fishes with : a smooth horizontal limb to the preoperculum, a basihyoid tooth plate, supralamellar tooth plates present on the outer face of the first four gill arches only ; with a single series of lateral line scales on the caudal fin, with the nostrils of each side widely separated, and a caudal fin skeleton in which there are two epural bones and a single uroneural.

Probably only one species, *P. waigiensis* (a second nominal species *P. macroptera* Günther, 1859, is almost certainly a synonym), widely distributed in the coastal waters of the Indo-Pacific.

LATES C. & V., 1828

TYPE SPECIES : *Perca nilotica*, L., 1758.

Latine fishes with the horizontal limb of the preoperculum produced into three or four (rarely more) large, flattened and triangular spines, no basihyoidal tooth plate but supralamellar tooth plates present on both the anterior and posterior faces of the first four gill arches, with three series of lateral line scales on the caudal fin, with the nostrils of each side close together, and a caudal fin skeleton with two epurals and two uroneurals.

Eight extant species (seven of which are African and confined to freshwaters, and one marine or estuarine and widely distributed in Indo-Pacific coastal waters) arranged in two subgenera :

LATES (LATES)

TYPE SPECIES : *L. niloticus* (L).

Species of the genus in which the posterior face of the lateral ethmoid has only a slight slope posteriorly, the dorsolateral parts of that bone are almost horizontally aligned, and the entire ethmovomerine region of the skull is not noticeably elongate. Four species : *L. calcarifer* (Indo-Pacific), *L. niloticus* (rivers of northern and western tropical Africa, and also in Lakes Chad, Albert and Rudolf [introduced into Lakes Victoria and Kioga]), *L. macrophthalmus* (Lake Albert only) and *L. longispinis* (Lake Rudolf only).

LATES (LUCIOLATES)

TYPE SPECIES : *Luciolates stappersi* Boulenger, 1914.

Species of *Lates* having a characteristically shaped and elongate ethmovomerine skull region in which the posterior face of the lateral ethmoid slopes backwards at a pronounced angle, and the dorsolateral aspects of that bone are directed ventrally at a steep angle. Four species, all endemic to Lake Tanganyika : *L. angustifrons*, *L. microlepis*, *L. mariae* and *L. stappersi*.

The single extinct genus is :

EOLATES Sorbini, 1970

TYPE SPECIES : *Lates gracilis* Agassiz, 1883.

See Sorbini, 1973, for full description, synonymies, etc.

Eolates, with one species (*E. gracilis*) and possibly a second, *E. macrurus* (Ag.), 1833, is known only from the lower Eocene deposits of Monte Bolca, northern Italy.

Eolates differs from *Lates* in the structure of its caudal fin skeleton (three epurals ; a well-developed neural spine on the second preural vertebrae), in having only a single series of lateral line scales (the median one) on the caudal fin, and in having a less deeply indented dorsal fin (see p. 70 above).

The phyletic relationships of Eolates within the Latinae are discussed on p. 71, where it is suggested that *Lates* and *Eolates* are sister taxa and should be placed in the Tribe Latini nov., the sister group of the Tribe Psammopercini nov. (a taxon containing only the genus *Psammoperca*).

ACKNOWLEDGEMENTS

Again, it is a pleasure for me to thank Drs Colin Patterson, Donn Rosen and Gareth Nelson for the numerous and illuminating discussions we have had on the centropomid fishes and on aspects of their anatomy in a broader context. To my colleague, Gordon Howes, goes my gratitude for the great amount of work and skill he has put into producing the figures illustrating this paper, and, as always, for his invaluable assistance in innumerable other ways. To Dr Thys van den Audenaerde go my thanks for lending me specimens of *Luciolates stappersi* from the Musée Royal de l'Afrique Centrale, Tervuren, to Dr Mary Burgis (the City of London Polytechnic) for her considerable efforts in getting material from Lake Tanganyika, and to my colleague, Dr Keith Banister, for examining the type of *Eolates gracilis* on my behalf.

REFERENCES

ALLEN, W. F. 1905. The blood vascular system of the Loricati, the mail-cheeked fishes. *Proc. Wash. Acad. Sci.* **7** : 27–157.

ALLIS, E. P. 1909. The cranial anatomy of the mail-cheeked fishes. *Zoologica, Stuttg.* **22** (57) : 1–219.

Bassani, F. 1889. Ricerche sui pesci fossili di Chiavon. *Atti Accad. Sci. fis. mat. Napoli* **2** (6) : 1–102.

Beadle, L. C. 1974. *The inland waters of tropical Africa.* viii+365 pp. London.

Berg, L. S. 1940. Classification of fishes, both recent and fossil. *Trav. Inst. zool. Acad. Sci. U.S.S.R.* **5** (2) : 87–517. (Russian and English texts. Reprint Edwards, Ann Arbor, Michigan, 1947.)

Bloch, M. E. 1792. *Naturgeschichte der ausländischen Fische,* **6.** Berlin.

Boulenger, G. A. 1914. Mission Stappers au Tanganyika-Moero. Diagnoses de poissons nouveaux. I. Acanthopterygians, Opisthomes, Cyprinodontes. *Revue zool. afr.,* **3.** 442–447.

—— 1915. *Catalogue of the freshwater fishes of Africa in the British Museum (Natural History),* **3** : xii+526. London.

Chávez, H. 1961. Estudio de una nueva especie de robalo del Golfo de México y redescripción de *Centropomus undecimalis* (Bloch) (Pisc., Centropom.). *Ciecia Mex.,* **21** (2) : 75–83.

Cuvier, G. L. C. F. G. & Valenciennes, A. 1828. *Histoire naturelle des poissons,* **2** : 490 pp. Paris.

Daget, J. 1954. Les poissons du Niger supérieur. *Mem. Inst. fr. Afr. noire,* **36** : 1–391.

Dunstan, D. J. 1959. The Barramundi *Lates calcarifer* (Bloch) in Queensland waters. *Tech. Pap. Div. Fish. Aust.* no. 5 : 1–22.

Fraser, T. H. 1968. Comparative osteology of the Atlantic Snooks (Pisces, *Centropomus*). *Copeia,* **1968** : 433–460.

Frost, G. A. 1934. Otoliths of fishes from the lower Tertiary formations of southern England. *Ann. Mag. nat. Hist.* (10), **13** : 426–433.

Gill, T. N. 1883. On the family Centropomidae. *Proc. U.S. natn. Mus.* **5** : 484–485.

Gosline, W. A. 1966. The limits of the fish family Serranidae, with notes on other lower percoids. *Proc. Calif. Acad. Sci.* **33** : 91–112.

Gosse, J.-P. 1956. Dispositions spéciales de l'appareil branchial des *Tilapia* et *Citharinus*. *Ann. Soc. zool. Belg.* **86** : 303–308.

Greenwood, P. H. 1951. Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. *Ann. Mag. nat. Hist.* (12), **4** : 1192–1201.

—— 1959. Quaternary fish-fossils. *Explor. Parc. natn. Albert Miss. J. de Heinzelin de Braucourt,* Brussels, **4** : 1–80.

—— 1973. Fish fossils from the late Miocene of Tunisia. *Notes Serv. géol. Tunis,* **37** : 41–72.

—— 1974. Review of Cenozoic freshwater fish faunas in Africa. *Ann. geol. Surv. Egypt,* **4** : 211–232.

—— & Howes, G. J. 1975. Neogene fossil fishes from the Lake Albert–Lake Edward Rift (Zaire). *Bull. Br. Mus. nat. Hist.* (Geol.), **26** : 69–124.

—— Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* **131** : 339–455.

Gregory, W. K. 1933. Fish skulls : A study of the evolution of a natural mechanism. *Trans. Am. phil. Soc.* **23** : 75–481.

Günther, A. 1859. *Catalogue of the fishes in the British Museum,* **1** : xxi+524. London.

Heckel, J. J. 1855. Neue Beiträge zur Kenntniss der fossilen Fische Osterreichs. *Denkschr. Akad. Wiss. Wien,* **11** : 187–274.

Holden, M. J. 1967. The systematics of the genus *Lates* (Teleostei: Centropomidae) in Lake Albert, East Africa. *J. Zool., Lond.* **151** : 329–342.

Holmgren, N. & Stensiö, E. A. 1936. Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. *In* : Bolk, L., Göppert, E., Kallius, E. and Lubbock, W. (Eds), *Handbuch der vergleichenden Anatomie der Wirbeltiere,* **4** : 233–500. Berlin and Vienna.

Jordan, D. S. 1923. *A classification of fishes including families and genera as far as known.* Stanford University Publications, University Series, Biological Sciences, **3,** no. 2 : i–x+77–243.

KATAYAMA, M. 1954. Systematic position of the genus *Glaucosoma*. *Bull. Fac. Ed. Univ. Yamaguchi*, **4**, no. 1 : 23–29.

—— 1956. On the external and internal characters of *Lates calcarifer* (Bloch), with its systematic position. *Bull. Fac. Ed. Univ. Yamaguchi*, **6**, no. 1 : 133–140.

KRAMBERGER, K. G. 1902. Palaeichthyologische Beiträge. *Mitt. Jb. K. ung. geol. Anst.* **14** : 1–21.

LAKE, J. S. 1971. *The freshwater fishes and rivers of Australia.* 61 pp. Melbourne.

LINDBERG, G. U. 1971. *Opredelitel' i kharakteristika semeĭstv ryb mirovoĭfauny.* Izdatel'stvo 'Nauka' Leningrad. (Translated as : *Fishes of the world.* Halstead Press, New York, 1974. 545 pp.)

McALLISTER, D. E. 1968. The evolution of branchiostegals and associated opercular, gular, and hyoid bones and the classification of teleostome fishes, living and fossil. *Bull. natn. Mus. Can.* no. 221 : xiv–239 pp.

MATSUBARA, K. 1955. *Fish morphology and hierarchy.* Pts I–III. 1605 pp. Tokyo, Ishizaki-Shoten.

MEEK, S. E. & HILDEBRAND, S. F. 1925. The marine fishes of Panama. Pt II. *Publs Field Mus. nat. Hist.* no. 226, Zool. Ser., **15** : 331–707.

MUNROE, I. S. R. 1961. *The marine and freshwater fishes of Ceylon.* 351 pp. Dept. of External Affairs, Canberra.

NELSON, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. nat. Hist.* **141** : 475–552.

NORMAN, J. R. 1966. *A draft synopsis of the orders, families and genera of recent fishes and fish-like vertebrates.* 649 pp. British Museum (Nat. Hist.), London.

PATTERSON, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Phil. Trans. R. Soc. B*, **247** : 213–482.

—— 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Phil. Trans. R. Soc. B*, **269** : 275–579.

PELLEGRIN, J. 1922. Poissons de l'Oubanghi-Chari recueillis par M. Baudon. Description d'un genre de cinq espèces et d'une variété. *Bull. Soc. zool. Fr.* **47** : 64–76.

POLL, M. 1953. Poissons non Cichlidae. *Result. scient. Explor. hydrobiol. Lac Tanganyika* (1946–1947), **3** (5A) : 1–251.

—— 1957. Les genres des poissons d'eau douce de l'Afrique. *Annls Mus. r. Congo Belge Ser.* 8°, *Sci. Zool.* **54** : 1–191.

REGAN, C. T. 1913. The classification of the percoid fishes. *Ann. Mag. nat. Hist.* (8), **12** : 111–145.

RICHARDSON, J. 1844. Ichthyology. *In* : Richardson, J. & Gray, J. E. (Eds), *The zoology of the voyage of H.M.S.* Erebus and Terror, *under the command of Capt. Sir J. C. Ross during* 1839–43. 139 pp. London.

RIVAS, L. R. 1962. The Florida fishes of the genus *Centropomus*, commonly known as snook. *Q. Jl Fla Acad. Sci.* **25** : 53–64.

ROGNES, K. 1973. Head skeleton and jaw mechanism in Labrinae (Teleostei: Labridae) from Norwegian waters. *Arbok Univ. Bergen Mat.-Naturv. Ser.* no. 4 : 1–149.

ROSEN, D. E. 1973. Interrelationships of higher euteleostean fishes. *Zool. J. Linn. Soc.* **53** (Suppl. 1) : 397–513.

SORBINI, L. 1973. Evoluzione e distribuzione del genere fossile *Eolates* e suoi rapporti con il genere attuale *Lates* (Pisces–Centropomidae). *In* : Studi e ricerche sui giacimenti terziari di Bolca. *Memorie Mus. civ. Stor. nat. Verona* (fuori Ser. 2), **2** (1) : 1–43.

STINTON, F. C. 1966. Fish otoliths from the London Clay. *In* : Casier, E., *Faune ichthyologique du London Clay* : 404–496. British Museum (Nat. Hist.), London.

WEBER, M., & DE BEAUFORT, L. F. 1929. *The fishes of the Indo-Australian Archipelago*, **5** : xiv+458. Leiden.

WEILER, W. 1929. Die mittel- und obereocäne Fischfauna Ägyptens mit besonderer Berücksichtigung der Teleostomi. *Abh. bayer. Akad. Wiss., Munich*, n.f. **1** : 1–57.

WORTHINGTON, E. B. 1929. New species of fish from the Albert Nyanza and Lake Kioga. *Proc. zool. Soc. Lond.* **1929** : 429–440.

—— 1932. Scientific results of the Cambridge Expedition to the East African Lakes, 1930–1. –2. Fishes other than Cichlidae. *J. Linn. Soc.* (Zool.), **38** : 121–134.

P. H. GREENWOOD, D.Sc.
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.)
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepède, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4·50.
4. HAYNES, J. R. Cardigan Bay Recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. Pp. 245; 33 Plates, 47 Text-figures. 1973. £10·80.
5. WHITEHEAD, P. J. P. The Clupeoid Fishes of the Guianas. Pp. 227; 72 Text-figures. 1973. £9·70.
6. GREENWOOD, P. H. The Cichlid Fishes of Lake Victoria, East Africa: the Biology and Evolution of a Species Flock. Pp. 134; 1 Plate, 77 Text-figures. 1974. £3·75. Hardback edition £6.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

GENERAL
1 5 APR 1
LIBRARY
NATURAL HIST

FOSSIL REPTILES FROM ALDABRA ATOLL, INDIAN OCEAN

E. N. ARNOLD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 2
LONDON : 1976

GENERA
15 APR
LIBRARY
ATURAL H

FOSSIL REPTILES FROM ALDABRA ATOLL, INDIAN OCEAN

BY

EDWIN NICHOLAS ARNOLD

Pp. 83–116 ; 3 *Text-figures,* 4 *Tables*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 2
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 29 *No.* 2 *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

ISSN 0007-1498

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 13 *April,* 1976 *Price* £2·25

FOSSIL REPTILES FROM ALDABRA ATOLL, INDIAN OCEAN

By E. N. ARNOLD

CONTENTS

	Page
SYNOPSIS	85
INTRODUCTION	86
Family TESTUDINIDAE – LAND TORTOISES	88
Geochelone	88
Family CROCODYLIDAE – CROCODILES	89
Crocodylus	89
Family GEKKONIDAE – GECKOES	90
Paroedura	90
Geckolepis	91
? *Phelsuma*	94
Family IGUANIDAE – IGUANID LIZARDS	95
Oplurus	95
Family SCINCIDAE – SKINKS	98
'*Scelotes*'	98
Mabuya	100
ORIGIN OF THE POINT HODOUL LIZARD DEPOSIT	101
COMPARISON OF ALDABRA REPTILES WITH THOSE OF NEIGHBOURING AREAS	104
HABITAT REQUIREMENTS OF EXTINCT ALDABRA REPTILES	106
POSSIBLE RESOURCE PARTITION BY EXTINCT ALDABRA REPTILES	107
BODY SIZE AND 'ISLAND GIGANTISM'	109
POSSIBLE CAUSES OF EXTINCTION	111
COMPETITIVE EXCLUSION	111
EXTERMINATION BY AN INVADING PREDATOR	112
LOSS OF ECOLOGICAL RESOURCES	113
COLONIZING ABILITY OF ALDABRA REPTILES	113
ACKNOWLEDGEMENTS	114
REFERENCES	114

SYNOPSIS

The present reptiles of Aldabra comprise only the giant tortoise, *Geochelone gigantea*, two geckoes, *Phelsuma abbotti* and *Hemidactylus mercatorius*, and the skink, *Cryptoblepharus boutonii*, but a richer and quite different fossil fauna has recently been discovered. Giant tortoises occur in most terrestrial deposits on the atoll and remains of crocodiles and lizards have been found in two: the Bassin Cabri Calcarenites (undated, but considerably older than 125 000 years B.P.) and cavity fillings in the Aldabra limestone at Point Hodoul formed since 100 000 years B.P. The Bassin Cabri Calcarenites contain remains of a crocodile similar to *Crocodylus niloticus* and of an iguanid lizard of the genus *Oplurus*. These also occur in the Point Hodoul deposits together with five other kinds of lizards, two or three of which are geckoes (a *Paroedura* similar to *P. sanctijohannis* and *P. stumpffi*, a *Geckolepis* close to *G. maculata* and what is possibly a *Phelsuma*) and two skinks (a '*Scelotes*' similar to '*S.*' *johannae* and a *Mabuya* very like *M. maculilabris*). The Point Hodoul lizard remains may be the food residue of a predator, perhaps an owl. The reptile fauna of Aldabra is much more similar to that of Madagascar and the Comores

Islands than to that of East Africa or of the Seychelles. Composition of the Point Hodoul fauna and the presumed requirements of some of its members suggest that conditions on Aldabra at that time may have been rather similar to those now occurring on the Comores. It is likely that the ecological requirements of the fossil forms were sufficiently different for them all to be able to coexist. Some of the fossils clearly differ in size from their closest modern relatives, both the *Geckolepis* and the *Oplurus* being very large; possible reasons for this are discussed. Aldabra was completely submerged after the laying down of the Bassin Cabri Calcarenites, but not since the Point Hodoul deposits were formed. Extinction of the reptiles found in the latter may have been largely caused by transient or permanent loss of ecological resources, although competition from the species existing on the atoll today could have been a minor factor. The possible importance of invading predators is difficult to assess. All the reptiles known from Aldabra seem to have been well adapted to the problems of transmarine colonization. There is evidence that the giant tortoises reached the island three times and the crocodile and *Oplurus* at least twice.

INTRODUCTION

THE study of island faunas has had a long history and is again fashionable, one of the most influential events in bringing this about being the appearance of *The theory of island biogeography* by MacArthur and Wilson in 1967. Among the topics that have recently received attention is the problem of what factors limit the number of species on islands and the importance of extinction rates in this process. A restriction on such investigations is the paucity of direct evidence of natural faunal change on islands. This is especially true in the case of reptiles. Instances are known where late Pleistocene or more recent island reptiles have become extinct (see, for instance, Etheridge, 1964, 1965, 1966 for the West Indies, Bravo, 1953 for the Canary Islands and Vinson & Vinson, 1969 for the Mascarenes), but often only part of the previous fauna has disappeared and there is frequently circumstantial evidence that human influences have been important in bringing such changes about. Situations where there has been an extensive faunal turnover in probably more natural conditions would consequently be of interest. Aldabra appears to be a case in point.

Aldabra is situated about 640 km east of the African mainland, about 380 km northeast of the Comores Islands and some 420 km northwest of Madagascar (see Fig. 1). It is a low atoll, being only about 10 m above sea level at its highest point, and is some 34 km long by 14·5 km wide. There is a large central lagoon and the total land area is 155 km^2. Much of the present surface consists of coral limestone, which is often covered by scrub. There are few natural large trees and the lagoon is fringed by mangrove. The present reptile fauna consists of giant tortoises (*Geochelone gigantea* Schweigger, 1812), two geckoes (*Hemidactylus mercatorius* Gray, 1842 and *Phelsuma abbotti* Stejneger, 1893) and the skink, *Cryptoblepharus boutonii* (Desjardins, 1831). None of these species is confined to the atoll and all of them have relatively wide distributions in the West Indian Ocean.

The island has been the subject of considerable scientific research by a series of expeditions organized by the Royal Society since 1966. Some of the results of this work have been published and a number of papers on the atoll form volume 260 of *Philosophical Transactions of the Royal Society of London, series B* (1971). Braithwaite, Taylor & Kennedy (1973) have given an account of the depositional and

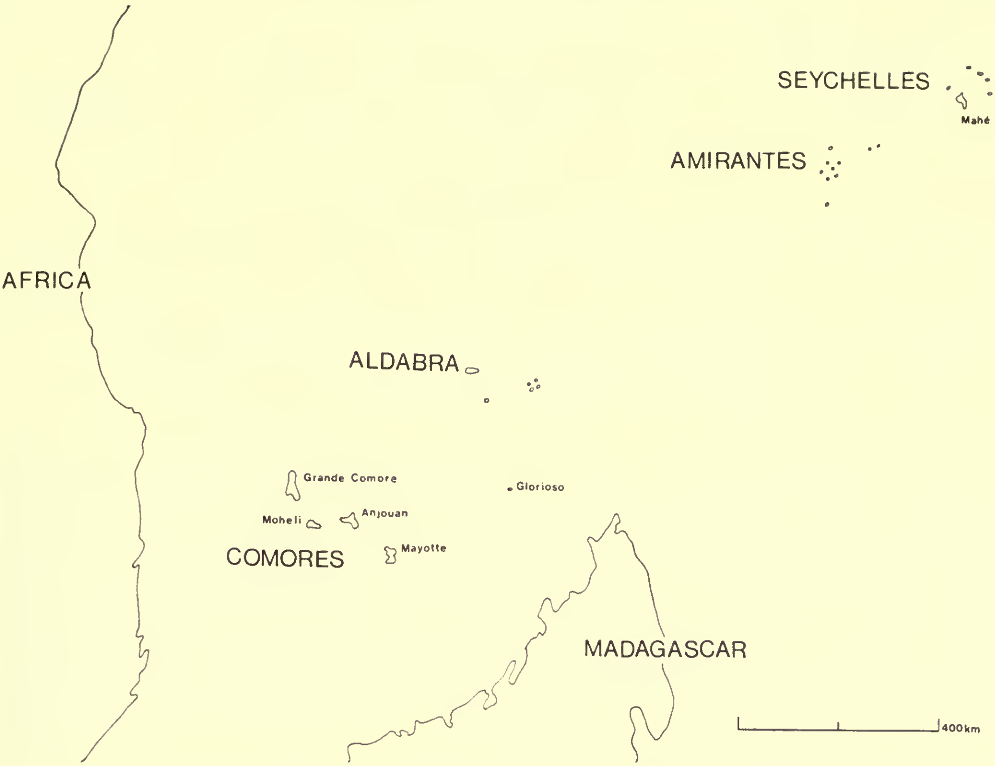


FIG. 1. West Indian Ocean, showing position of Aldabra and other nearby islands mentioned in text.

erosional history of Aldabra. During investigations on the island, Dr J. D. Taylor of the British Museum (Natural History) collected substantial amounts of fossil material including the reptiles that form the basis of this paper. Large numbers of tortoise remains were also observed *in situ* but could not be extracted for detailed examination.

Tortoises occur in many of the terrestrial deposits of Aldabra (Braithwaite *et al.*, 1973). Lizards and crocodiles have also been found, but only in two deposits, the Bassin Cabri Calcarenites and cavity fillings in the Aldabra Limestone at Point Hodoul (see Fig. 2). The Bassin Cabri Calcarenites are of unknown age, but they are older than the Aldabra Limestone which has yielded dates by the ^{230}Th/^{234}U method of 118 000 to 136 000 ± 9000 years B.P. (Thompson & Walton, 1972). The Point Hodoul deposits were probably formed since 100 000 years B.P. (Braithwaite *et al.*, 1973). Most of the reptile fossils consist of dissociated bones, few of which are intact. However, although many are broken, the majority are not obviously eroded and are therefore identifiable. This is especially true of the lizard bones, over 1000 of which have been determined.

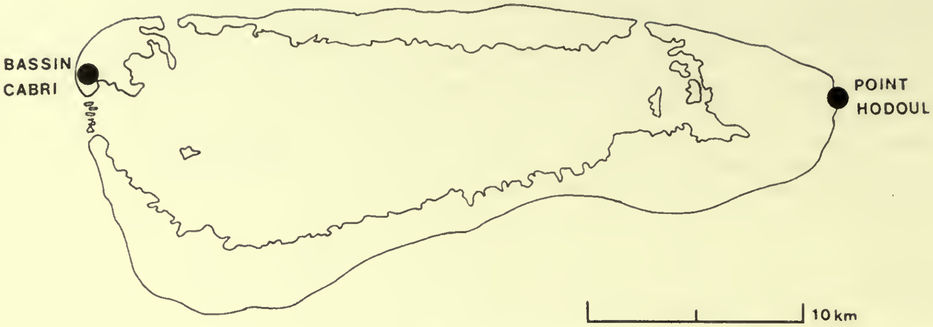


FIG. 2. Aldabra Atoll, showing the two main localities where fossil reptiles were collected.

Because of the relatively recent age of the deposits, it was assumed as a working hypothesis that the species represented would probably have close relatives amongst the extant reptiles of the West Indian Ocean, or of the Ethiopian region as a whole. Initial identification was consequently attempted by comparison with the present fauna of that area and it proved possible to find good matches for nearly all the material by this means. Two difficulties in assessing the fossils were the lack of really adequate comparative material in museum collections and the need for taxonomic revision of some of the groups concerned (for instance, the scincine lizards of Madagascar and nearby islands – see Greer, 1970b). These constraints have limited the preciseness of identification in some cases.

As nearly all the fossils are generally like known modern forms, they are not described in detail below. Instead, comment is restricted to diagnostic characters and to any features in which the fossils differ from their modern counterparts. In most cases, the names used for lizard skull elements follow Oelrich (1956). Because many of the fossils are broken, numbers of particular bones, given in the lists of material examined, tend to be minima.

Order TESTUDINES
Chelonians

Family **TESTUDINIDAE**
Land tortoises

GEOCHELONE Fitzinger, 1835

MATERIAL REFERRED. *Point Hodoul cavity fillings. Registered number*: R8762. Numerous fragments, especially eroded limb bones.

Tortoise remains were observed in nearly all the terrestrial deposits on Aldabra.

IDENTIFICATION. This material has not been examined in detail, but it resembles *Geochelone gigantea* (Schweigger, 1812), the giant tortoise that occurs on Aldabra at the present time.

Order CROCODYLIA
Crocodilians

Family **CROCODYLIDAE**
Crocodiles

Crocodylus Laurenti, 1768

Material referred. *Bassin Cabri Calcarenites. Registered number*: R8885. Tooth: 1.

Point Hodoul cavity fillings. Registered number: R8763–98. Premaxillae: right – 2, left – 1. Maxilla: 1 (fragment). Jugals: right – 5, left – 6. Frontals: 3. Frontal + parietal: 1. Parietal: 1. Parietal + supraoccipital: 1. Squamosals: right – 4, left – 1. Pterygoids: right – 1, left – 1. Ectopterygoids: right – 1, left – 2. Dentary fragments: 11. Isolated teeth: 6. Vertebrae: 2 (fragments). Caudal chevrons: 2. Osteodermal scutes: 45.

Identification. The Point Hodoul remains include premaxillae. These show a clear lateral notch that in life would have received the enlarged fourth mandibular tooth. The bones also suggest that the animals from which they came had snouts that were neither conspicuously narrowed nor laterally expanded. Amongst recent crocodilians, this combination of features is restricted to *Crocodylus*. Comparison of the two extant African species of the genus shows that the fossils are very similar to modern *C. niloticus* Laurenti, 1768, although some elements, e.g. the jugals, appear more robust than those of equivalent-sized mainland African animals with which they were compared. On distributional grounds, *C. niloticus* is the most likely modern crocodile to have reached Aldabra, for it is the only species in eastern Africa. It is also known to have been present in the Seychelles and exists on the Comores and on Madagascar.

Estimated number of individuals in sample. On the basis of the commonest element, viz. the jugal, there must have been at least six individuals represented in the Point Hodoul sample.

Estimated body size. Comparison of the fragments with intact skulls of modern African specimens suggests that the largest came from crania about 310 to 320 mm in length (snout-tip to medial posterior border of the supraoccipital bone). Bellairs (1969) has found that the ratio of skull length to total length is about 1 : 7·5 in *C. niloticus* and that this holds over a wide variety of sizes. On this basis, the largest Aldabra fragments would have belonged to an animal 2·33 to 2·40 m long. This is much smaller than the known maximum for mainland African populations, although obviously the small sample available cannot exclude the possibility that the Aldabra animals grew bigger. However, the robustness of some of the bones could indicate maturity and if this is so, the atoll population may have been characterized by small body size. This would not be unexpected, especially as 'dwarf' populations of this species are known from some areas of East Africa (Cott, 1961).

Suborder SAURIA
Lizards

Family **GEKKONIDAE**
Geckoes

Paroedura Günther, 1879

Material referred. *Point Hodoul cavity filling. Registered number*: R8849–77. Premaxillae: 18. Maxillae: right – 25 (one complete), left – 21. Conjoined nasals – 4. Prefrontals: right – 18, left – 16. Frontals: 28. Postfrontals: right – 23, left – 15. Parietals: right – 11, left – 17. Pterygoids: right – 11, left – 13. Quadrates: right – 21, left – 19. Dentaries: right – 21, left – 18. Coronoids: right – 16, left – 12. Proximal jaws: right – 14, left – 14. Axis: 1. Cervical vertebrae: 10. Dorsal vertebrae: 86 approx. Sacrum: 1. Basal caudal vertebrae: 22. Autotomic caudal vertebra: 1. Scapulocoracoids (incomplete): right – 1, left – 3. Scapulae: left – 1. Pelvic girdles (incomplete): right – 9, left – 7. Humeri: more or less intact, right – 1, left – 1; proximal sections, right – 13, left – 6; distal sections, right – 12, left – 6. Femora: proximal sections, right – 18, left – 21; distal sections, right – 7, left – 7. Tibiae: right – 6, left – 3.

Identification. Certain elements of this material are clearly of gecko origin. The frontals, which are undivided, have lateral downgrowths that meet and fuse ventrally to form a cylinder and the vertebrae are amphicoelous. Amongst lizards, both these features are confined to the Gekkonidae, although not universal in them.

Other striking characteristics of these fossils include the following: heavy ossification of the dorsal skull bones; presence of a well developed, 'sculptured' ornamentation of their outer surfaces; conjoined nasal bones and prominent notching of the anterior lateral edges of the parietals to take the posterior section of each postfrontal. Within the geckoes, this combination of characters seems to be limited to nine nominal species now confined to Madagascar and the Comores Islands. These have usually been included in *Phyllodactylus* Gray, 1828, but Dixon & Kroll (1974) have recently transferred them to a separate genus, *Paroedura*. As the species concerned do appear to form a natural assemblage, this course is followed here, although the authors' implication that *Paroedura* may have had a separate origin from *Phyllodactylus*, as they understand it, and that the two groups evolved similar foot structure independently is unproven. It seems just as likely that *Paroedura* is a derivative of the more typical members of *Phyllodactylus*.

Paroedura is a quite tightly knit group of species, the interrelationships of which have not yet been fully worked out. This makes it difficult to decide with certainty which of the modern forms are most closely related to the fossil Aldabra material, but the latter has most superficial likeness to *P. sanctijohannis* Günther, 1879 of the Comores Islands and *P. stumpffi* (Boettger, 1878) of North Madagascar and Nossi Bé. It resembles the former closely in the degree and pattern of sculpturing on the dorsal skull bones, in parietal shape (distinctly curved transverse section that is convex above and a distinctly sinuous posterior border) and in having very broad quadrate bones. However, the frontals are less obviously concave above than in the modern specimens of *P. sanctijohannis* examined (from Anjouan and Grande Comore) and in this respect are more like *P. stumpffi*, although the fossils resemble this species less in details of parietal shape and sculpturing. *P. gracilis* (Boulenger, 1896) is also rather similar, but its parietal has a straighter posterior border and its frontal is more deeply concave above. *P. picta* (Peters, 1854) has a much narrower quadrate and rather coarser 'sculpturing'. The 'sculpturing' in *P. androyensis* (Grandidier, 1867) also seems to be coarser than in the fossils and the parietal is more rectilinear with a flatter transverse section. *P. bastardi* (Mocquard, 1900) shares the latter feature and its 'sculpturing' is coarser still; also the crest on the proximal anteroventral face of the humerus, for the pectoralis muscle, is set almost at right angles to the ventral face of the bone and its anterior face is slightly concave with a well developed anterodorsal ridge forming its upper border. In *P. oviceps* (Boettger, 1881) the parietal is flatter than in the Aldabra material with a less sinuous posterior border and its surface sculpturing is weaker.

Of the two remaining nominal species of *Paroedura*, the unique type of *P. homalorhina* (Angel, 1936) no longer exists (J. Guibé, personal communication) and *P. guibae* Dixon & Kroll, 1974 has not been examined by me.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. There are 28 recognizable frontal bones of *Paroedura*, so at least this number of individuals must be represented in the sample.

ESTIMATED BODY SIZE. On the basis of comparison of limb bones and frontals, it seems that the Aldabra *Paroedura* grew to about 60 mm from snout to vent, or a little more. This compares with a maximum length of 70 mm for modern *P. stumpffi* and 67 mm for *P. sanctijohannis* (see Angel, 1942).

Geckolepis Grandidier, 1867

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number*: R8828–48. Premaxillae: 3. Maxilla: left – 1. Prefrontals: left – 3. Frontals: left – 1 (anterior section only). Parietals: right – 2 fragments (anterior lateral section, central lateral section), left – 3 fragments (2 central lateral sections, posterior lateral section). Palatine: left – 1. Pterygoids: right – 1 fragment, left – 4 fragments. Quadrates: left – 2. Dentaries: right – 1 (anterior section only), left – 1 (anterior section absent). Coronoids: right – 1, left – 1. Vertebral centra: 5. Sacrum: 1. Scapulocoracoids: right – 2, left – 2. Pelvic girdles: right – 2, left – 1. Humeri: more or less intact, right – 1; shafts, right – 4, left – 2; proximal section, left – 1; distal section, left – 2. Femora: proximal section, left – 2; distal section, right – 2, left – 2.

IDENTIFICATION. These fragments come from a gecko considerably larger than the Aldabra *Paroedura* discussed above. Initial tentative allocation to the Gekkonidae was based on a number of suggestive, but not fully diagnostic features, for instance the dentary is lightly built with a closed Meckel's groove and a very rounded lingual face. But, because the remains are so fragmentary, definite family assignment really depends on their detailed resemblance to a particular gecko species.

The more distinctive features of the material are as follows :

1. The largest premaxilla has an estimated 13 teeth. The nasal process is rather broad and is slightly constricted at the level where it would pass between the external nasal openings of the skull, but it expands again above this. In the most complete premaxilla, the process then rapidly tapers to an obtuse point.

2. The maxilla has a broad palatal shelf and the nasal process (i.e. the dorsally directed lamina that forms part of the side of the snout) rises smoothly from the tooth-bearing body of the bone with no pronounced inward 'step' just anterior to the orbit.

3. The anterior lateral fragment of the parietal is peculiar in that the angle between the fronto-parietal suture and the anterior section of the lateral margin of the bone is more than a right angle, whereas in most geckoes it is less (see Fig. 3).

4. From the fragments available, it is apparent that the upper surface of each parietal is distinctly convex above the descending flange of this bone, but lateral to this it is slightly concave. The convexity extends as a poorly defined ridge that curves inwards and backwards towards the posterior midline of the skull. From

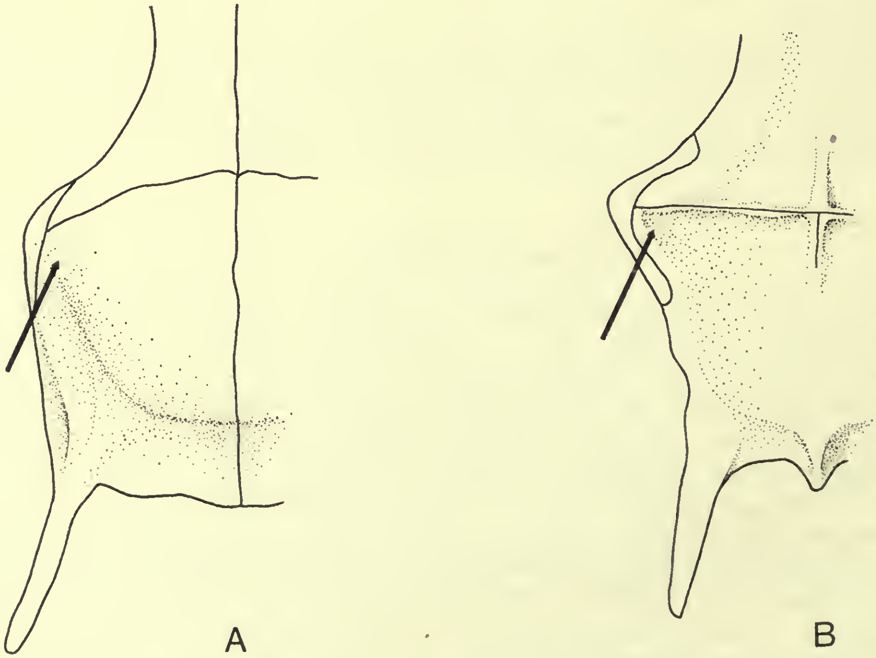


Fig. 3. Dorsal views of the left posterior areas of two gecko skulls, showing difference in shape of the anterolateral region of the parietal (arrowed). A. *Geckolepis maculata* (based on BM 91.6.30.1). B. *Homopholis fasciata erlangeri* (based on BM 1931.7.20.255).

this ridge, an even less prominent one runs along the proximal upper surface of the supratemporal process of the parietal.

5. The outer surfaces of all the fragments of the superficial bones of the skull are either smooth and unornamented, or they have a weak pattern of shallow, thin grooves.

6. The quadrates have a very slender posterior crest. This is quite strongly and evenly curved (more so than in Aldabra *Paroedura*).

7. The anterior upper border of the ilium does not rise very abruptly, or recurve forwards, as it does in many geckoes.

8. The humerus is more robust than in the majority of geckoes. The crest on the proximal anteroventral surface of this bone is set almost at right angles to the ventral surface and its anterior exposure is strongly concave.

Examination of a wide range of Ethiopian and West Indian Ocean gekkonid lizards shows that this combination of features is approached closely only in the genus *Geckolepis*, which is now restricted to Madagascar and the Comores. The apparently related genus, *Homopholis* Boulenger, 1885, differs in having a distinct 'step' in the outer surface of the maxilla, just anterior to the orbit. Also, the fronto-parietal suture of *Homopholis* forms an acute angle with the anterior lateral edge of the parietal bone and there is no concavity on the forward surface of the proximal anteroventral crest of the humerus (all features confirmed on specimens of *H. walbergii* (Smith, 1849) and on *H. fasciata erlangeri* Steindachner, 1906 ; presence of a maxillary 'step' and the shape of the parietal were also checked on the type of *H. heterolepis* Boulenger, 1896). The more distantly related, widespread West Indian Ocean genus *Phelsuma* Gray, 1825 also differs in parietal shape. Furthermore, the premaxilla usually has a slender nasal process, the palatine shelf of the maxilla is typically rather narrow, the quadrate is usually more robust and the anterior upper border of the ilium rises abruptly or is recurved.

Within *Geckolepis*, the Aldabra material was compared with the largest extant species, *G. maculata* Peters, 1880 of Madagascar and the Comores, and with three of the four remaining species, all of which are restricted to Madagascar, viz. *G. anomala* Mocquard, 1902, *G. polylepis* Boettger, 1893 and *G. typica* Grandidier, 1867. Of these, it resembles *G. maculata* most closely. However, the fossils exhibit some mainly minor differences from the small sample of *G. maculata* available for comparison ($n = 3$) ; these are listed below :

1. The Aldabra fragments are distinctly larger than corresponding elements in modern *G. maculata*.

2. The nasal process of the premaxilla is slightly more constricted at the level where it would pass between the external nasal openings of the skull.

3. In modern material examined, the inner surface of the dentary swings slightly, but clearly, upwards from the base of the tooth-row before curving downwards to form the lingual surface of the bone. In the fossil dentary sections, the upward swing is less marked.

4. The anterior upper edge of the ilium curves upwards rather less than in compared modern material.

5. The crest on the proximal anteroventral surface of the humerus is better developed and its anterior exposure is more strongly concave. Also, the bone is more precisely moulded.

6. This is true of the proximal section of the femur as well. In addition, the femoral head has a more pronounced neck which has better developed ridges on its posterior and ventral surfaces.

It is possible that some or all of differences 2 – 6 are merely allometric concomitants of larger size. If they were due to allometric change, it might be expected that trends towards the conditions found in the Aldabra material would be apparent in a series of modern *Geckolepis* of increasing size, although absence of such trends could merely mean that the changes would only begin to be apparent at sizes larger than those attained today. In fact, only the expected changes in the humerus can be detected in the small series of *G. maculata* and *G. anomala* available. Another less direct indication that allometric growth might be responsible for some of the characters of the fossils would be the presence of similar differential growth processes in a related form that grows as large as the Aldabra animals. When *Homopholis walbergii* of assorted sizes were examined, changes in the femur similar to those expected in *Geckolepis* were found.

Although the features of the humerus and femur that distinguish the fossil *Geckolepis* of Aldabra from modern *G. maculata* may be due to allometric change, there is no evidence that the other characteristics of this material (i.e. differences 2–4) are due to this factor. However, they are relatively trivial and on their own, or even in conjunction with greater body size, do not seem to provide adequate grounds for recognizing the Aldabra material as a distinct form, especially as the sample of modern *G. maculata* available is so small and the Aldabra remains are so fragmentary.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. There are five right humeri, the commonest element present. But there is also a distal section of a left humerus that is smaller than any of the right ones, so at least six individuals must be represented.

ESTIMATED BODY SIZE. Calculations based on the sizes of fossil humeri and femora, compared with those of modern animals, suggest that the largest fossil *Geckolepis* were 90 to 100 mm from snout to vent. This contrasts with a present apparent maximum of 70 mm (Angel, 1942).

? ***Phelsuma*** Gray, 1825

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number*: R8878. Maxilla: left – 2 fragments (anterior section, section from just below lachrymal area). Dentaries: right – 1 fragment, left – 1 fragment (both from middle of bone).

IDENTIFICATION. The dentary fragments are lightly built and pleurodont with closed Meckel's grooves. The cylindrical body of the bone shows little dorsoventral taper along its length, its lower edge is almost straight and the lingual face is strongly rounded. The labial wall extending upwards from the dentary cylinder is very high compared with the depth of the latter and the labial face of the bone has a strongly curved transverse section. On this face, the mental foramina are situated considerably nearer the upper than the lower border of the dentary. The maxillary fragments indicate that the palatine shelf is narrow and concave beneath, at least in the area ventral to the lachrymal bone.

These fossils are not like the bones of the other species represented in the Point Hodoul deposit. The general facies of the dentary (light build, closed Meckel's groove, rounded lingual surface and straight lower border) suggests gecko origin. Certainly, it does not resemble the dentary of any of the lygosomine skinks found in the area that were examined, although these also have closed Meckel's grooves. Among those checked was *Cryptoblepharus boutonii* (Desjardins, 1831), which occurs on Aldabra today. In this species, the dentary is considerably narrower lateromedially and the lingual face is more flattened than in the fossils.

Although the bones could not be precisely matched with any of the many West Indian Ocean and Ethiopian geckoes compared with them, they do have a general resemblance to the smaller species of *Phelsuma*. However, none of the members of this genus examined* have the mental foramina placed so close to the upper margin of the dentary. This feature and the very restricted taper of the cylindrical body of the bone distinguish the fossils from *P. abbotti*, which is now present on Aldabra.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. Possibly only one individual is represented.

ESTIMATED BODY SIZE. The very fragmented nature of the material makes this difficult to assess, but the remains probably come from a lizard not more than 50 mm from snout to vent.

Family **IGUANIDAE**

Iguanid lizards

Oplurus Cuvier, 1829

Bassin Cabri Calcarenites

MATERIAL REFERRED. *Registered number* : R8883–84. Maxilla : right – 3 incomplete sections (complete dental arcade, but nasal and palatine processes absent ; section lacking most of dental arcade ; posterior process with teeth). Dentary : right – 1 (short anterior section), left – 1 (posterior section). Isolated tooth – 1.

IDENTIFICATION. The maxilla with a complete dental arcade has a tooth-row that is about 21 mm long. The teeth are pleurodont and all, except the most anterior, have flattened, more or less trilobed crowns : the largest are about 4 mm long. In the other, smaller, maxilla a well-developed, flat, triangular palatine process is present arising from about the middle of the bone. It is also apparent from the shape of the nasal process that the posterior border of the nasal orifice of the skull rose steeply. The two dentary fragments show that Meckel's groove is unclosed anteriorly and posteriorly although the middle section is not represented.

---

* Species of *Phelsuma* examined: *P. abbotti* Stejneger, 1893; *P. andamanensis* Blyth, 1860; *P. astriata* Tornier, 1901; *P. barbouri* Loveridge, 1942; *P. breviceps* Boettger, 1894; *P. cepediana* (Merrem, 1820); *P. dubia* (Boettger, 1881); *P. edwardnewtoni* Vinson & Vinson, 1969; *P. guentheri* Boulenger, 1885; *P. laticauda* (Boettger, 1880); *P. lineata* Gray, 1842; *P. madagascariensis* (Gray, 1831); *P. mutabilis* (Grandidier, 1869); *P. trilineata* Gray, 1842; *P. v-nigra* Boettger, 1913.

A pleurodont maxillary tooth-row of 21 mm is rare amongst present-day lizards of the Ethiopian region and the West Indian Ocean. Extant forms with maxillae approaching or exceeding this size include only monitors (*Varanus* Merrem, 1820) and large cordylids (*Gerrhosaurus* Wiegmann, 1828, *Zonosaurus* Boulenger, 1887), but these do not possess the trilobed teeth, fairly large palatine process and general habitus of the fossil material. The same is true of two recently extinct island lizards that grew large, the skink *Didosaurus mauritianus* Günther, 1877 of Mauritius and the gecko *Phelsuma gigas* (Liénard, 1842) of Rodriguez. Both of these also had fully closed Meckel's grooves. Modern relatives of the large Aldabra lizard must therefore be sought amongst smaller forms. In fact, the only species that have the characteristic features of the fossils are the members of the iguanid genus *Oplurus*, now known only from Madagascar and Grande Comore. The largest individual of the group examined in this study, an *O. cuvieri* 131 mm from snout to vent (BM 1930.7.1.149), has a maxillary tooth-row only 16·3 mm long.

No formal study of the interrelationships of the six species of *Oplurus* appears to have been made, but on superficial appearance they fall into two groups: (1) *O. quadrimaculatus* (Duméril, 1851), *O. saxicola* Grandidier, 1869 and the generally similar *O. fierinensis* Grandidier, 1869 and *O. grandidieri* (Mocquard, 1900); (2) *O. cuvieri* (Gray, 1831) – a senior synonym of *O. sebae* Duméril & Bibron, 1837 (see Savage, 1952) – and *O. cyclurus* (Merrem, 1820). The members of the first group have more flattened heads and bodies than those in the second and the species that have been examined here, viz. *quadrimaculatus* and *saxicola*, also differ from *cuvieri* and *cyclurus* in having a more concave lingual profile to the lateral cheek teeth and the maxillary border of the posterior edge of the external nasal opening of the skull curving more gently upwards. In the two latter features, the Aldabra maxillaries agree with *O. cuvieri* and *O. cyclurus*. The shape of the nasal process of the smaller maxillary and of its palatine process is much more like *cuvieri* than *cyclurus*, so on present limited evidence, the former species appears closest to the fossil material. At the present time, *O. cuvieri* occurs in West and Northwest Madagascar and on Grande Comore.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. As there are substantial fragments of two right maxillae that include homologous areas and are of different sizes, at least two individuals must be represented.

ESTIMATED BODY SIZE. The maxilla with teeth is about 21 mm long, while that of a modern *O. cuvieri* 131 mm from snout to vent is 16·3 mm. Making no allowance for allometric growth, this would suggest a snout to vent length for the lizard from which it came of about 170 mm. The smaller maxilla, on the basis of the same sort of calculation, might have come from an animal about 157 mm from snout to vent.

Point Hodoul cavity filling

MATERIAL REFERRED. *Registered number*: R8879-82. Maxilla: right – 1 fragment (short anterior section). Small tooth-bearing fragments: 4. Cervical vertebra: 1 (probably third or fourth). Dorsal vertebrae: fragment, 1 (probably from region immediately anterior to sacrum. This last specimen is the one referred to in Braithwaite *et al.* (1973) as 'possibly the vertebra of a varanid lizard'.)

IDENTIFICATION. This material is even more fragmentary than that from the Bassin Cabri Calcarenites, but again it is obvious that a large lizard with pleurodont, trilobed teeth is represented, the biggest teeth being 4·7 mm long. The remains correspond closely to *Oplurus*. The anterior section of the maxilla includes the premaxillary process, i.e. that part of the maxilla the superior surface of which forms the lower rim of the external nasal opening of the skull. This surface is concave and rises abruptly, medial to the anterior inferior alveolar foramen, to form a well developed ridge that declines anteriorly. This is similar to the condition found in *O. cyclurus* and particularly *O. cuvieri*. It is not like that present in the members of the *O. quadrimaculatus* group examined where the medial ridge is far less abrupt.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. The remains may only represent a single individual as none of the elements is duplicated, but see below.

ESTIMATED BODY SIZE. When compared with an *O. cuvieri* 125 mm from snout to vent, the linear dimensions of the fossil maxillary fragment were found to be about 1·7 to 1·8 times as great as the equivalent area of the modern individual while linear dimensions of the vertebrae were greater by a factor of over 2. This discrepancy might be due either to the maxilla and vertebrae coming from different individuals or, more probably, to negative allometric growth of the maxilla relative to the vertebrae. The measurements suggest that the *Oplurus* from the Point Hodoul cavity filling was probably at least 210 mm from snout to vent and possibly larger than 250 mm. *O. cuvieri* may have a tail length 1·7 times that of the body (Angel, 1942), so if the analogy to this species holds, the fossil lizard could have been between 570 and 680 mm in total length.

Differences from modern Oplurus cuvieri

Although the fossils agree best with *O. cuvieri* among living species of *Oplurus*, there are some distinct differences between them and modern material examined. Apart from their greater size, they differ in the following ways:

Bassin Cabri Calcarenites. The nasal process of the maxillary is more rugose with a rougher outer surface.

Point Hodoul cavity filling. 1. The anterior section of the maxilla has a very distinct ridge separating the superior and lateral surfaces of the premaxillary process; this is markedly undercut anteriorly.

2. The cervical vertebra has the sagittal ridge running along the underside of the centrum very well developed and the area on each side of it much more concave than in *O. cuvieri*.

3. The dorsal vertebra has a distinct but ill defined ridge running transversely from the hind edge of the articular surface of each prezygopophysis towards the neural spine. This ridge accentuates the hollow between the leading edge of the neural arch and the prezygopophysis.

As the Aldabra *Oplurus* was so much bigger than modern *O. cuvieri*, the differences might be expected to have an allometric component. However, when large and small examples of both *O. cuvieri* and *O. cyclurus* were examined, little evidence of the expected allometric trends could be found, although the sagittal ridge on the undersides of the third and fourth cervical vertebrae tends to become somewhat better developed. A series of the large iguanid, *Iguana iguana* (Linnaeus, 1758), also shows some limited change in the shape of the cervical vertebrae, but not in the other characters that distinguish the Aldabra *Oplurus* material. Since these features are well marked and there is no clear evidence that they include a large allometric component, it is possible that the fossils do represent a taxon distinguishable from modern *O. cuvieri*, but because the remains are so fragmentary, it seems unnecessary to give it formal recognition at the present time.

Family **SCINCIDAE**
Skinks

'*Scelotes* Fitzinger 1826'

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number*: R8799–8818. Maxillae: right – 5, left – 3. Prefrontals: right – 3, left – 1, Frontals: right – 8, left – 9. Parietals: 7. Conjoined vomers: 1. Pterygoids: right – 2, left – 2. Basioccipitals: 2 (one fragmentary). Quadrates: right – 6, left – 5. Dentaries: right – 19, left – 14. Proximal sections of mandibles: right – 9, left – 4. Axes: 3. Third cervical vertebrae: 2. Dorsal vertebrae: 223 approx. Sacra: 2. Basal caudal vertebrae: 2. Autotomic caudal vertebrae: 57 approx. Scapulocoracoid: right – 1. Pelvic girdles: right – 5, left – 3. Humeri: intact, left – 1; proximal sections, right – 4, left – 4; distal section, left – 1. Femora: intact, right – 2, left – 3; proximal sections, right – 4, left – 10; distal sections, right – 7, left – 3.

IDENTIFICATION. Dentaries in this sample are robust with Meckel's groove open throughout their lengths. The teeth are coarse, peg-like and pleurodont with crowns that are slightly compressed labio-lingually. In the largest specimens, about 18 teeth, or rather more, are present and the tooth-row is approximately 5·5 mm long. Among the lizards of the Ethiopian region and West Indian Ocean, pleurodonty rules out agamids and chameleons and size alone excludes varanids. The two iguanid genera in the area (*Oplurus* and *Chalarodon* Peters, 1854) have trilobed lateral teeth and partly closed Meckel's grooves. Geckoes can also be excluded as Meckel's groove is completely closed in this family. By elimination, it therefore seems probable that the mandibles are from a scincomorph lizard. This is supported by aspects of the associated remains, such as the even osteodermal layer on the frontals and parietals and the indications of large scales on the latter.

There are three scincomorph families in the area, namely the Lacertidae, Cordylidae and Scincidae. The fossils differ from members of the first two in the following ways:

1. The parietals have simple down-turned lateral edges, there being no tendency to extend laterally to form a partial roof over the supratemporal foramen.

2. In the midline area, the parietal projects backwards on each side of the *fossa parietalis* as two well developed and broadly separated processes.

3. The weakly indicated pattern of scales on the parietal osteodermal layer is unlike that of lacertids or cordylids.

However, all the features of the fossils occur in some Scincidae, so they have been assigned to this family.

Within the skinks, the material is quite unlike the aberrant Acontinae and Feylininae and differs from Ethiopian and West Indian Ocean Lygosominae examined in having an open Meckel's groove and paired frontals. Both these features are typical of the remaining subfamily, the Scincinae (Greer, 1970a). Scincinae of the Ethiopian region and the islands of the West Indian Ocean have been reviewed by Greer (1970b). This author states that a relatively small interparietal scale is confined to *Proscelotes* de Witte & Laurent, 1943 and to *Sepsina* Bocage, 1866 on the African mainland, and to the endemic scincines of the West Indian Ocean including Madagascar. The Aldabra material has a small interparietal scale indicated in the osteodermal layer of the parietal bone and, as it bears no close resemblance to *Proscelotes* or *Sepsina*, it seems reasonable to assume that it is nearest to the Indian Ocean forms. Of these, the species endemic to the Seychelles and Mascarene islands that were originally placed in *Scelotes* but are now assigned to separate genera can be eliminated from further consideration. All three, viz. *Gongylomorphus bojerii* (Desjardins, 1831), *Pamelaescincus gardinieri* (Boulenger, 1909) and *Janetaescincus braueri* (Boettger, 1896), have flatter parietals than the Aldabra specimens, with less lateral down-turning and at least a tendency to extend sideways over the supratemporal foramen. They also have much finer dentition. The remaining West Indian Ocean forms are confined to Madagascar and nearby islands (Glorioso and the Comores). The 39 or so nominal species have been assigned to a number of genera, the majority being placed in *Scelotes*. According to Greer, the whole group is in need of thorough revision and may not be particularly closely related to the *Scelotes* of the African mainland, which include the type species of the genus. The restricted understanding of the group, together with the fact that it is poorly represented in museum collections, precludes a comprehensive comparison with the Aldabra material, but the latter does seem very similar to the two medium-sized, short-legged populations that now occur respectively on the Comores and on Glorioso and are named as '*Scelotes*' *johannae* (Günther, 1880) and '*S.*' *valhallae* (Boulenger, 1909). The most obvious difference is that the Aldabra specimens have coarser dentition.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. On the basis of the commonest element present, the right mandible, at least 19 individuals are represented.

ESTIMATED BODY SIZE. Calculations based on the relative sizes of vertebrae, frontals, parietals and femora of the Aldabra material and of '*S.*' *johannae* and 'S.' *valhallae* suggest that the largest Aldabra '*Scelotes*' in the sample grew to about 90 mm from snout to vent compared with at least 110 mm for '*S.*' *johannae* and at least 104 mm for '*S.*' *valhallae.*

Mabuya Fitzinger 1826

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number*: R8819–27. Maxillae: right – 2 (one with posterior tip missing, one with anterior section missing), left – 1 (anterior section missing). Frontals: 2 sections (posterior section, central section including left lateral flange). Jugal: right – 1. Quadrate: right – 1. Dentary + splenial: left – 1 (posterior sections of bones and dentary tip absent). Dentary: left – 1 (middle section only). Articular section of mandible: right – 1. Dorsal vertebrae: 5. Humeri, proximal sections: right – 1, left – 1. Femur, distal section – 1.

IDENTIFICATION. The frontals are unpaired but their lateral flanges are not extended ventrally to form a tube, so they are unlikely to be of gecko origin. Both sections are covered dorsally by an even osteodermal layer and in the posterior one there are grooves representing the sutures between a large frontal scale and large paired frontoparietals, the suture between the latter being oblique. The general form of these frontals, their even osteodermal layer and the large scales indicated in it all suggest that they are from a scincomorph lizard. Cordylids can be discounted at once as they have paired frontals and this is also true of many lacertids, those showing the unpaired condition usually have the frontal quite strongly narrowed medially and the suture between the frontoparietal scales is more or less sagittal, not oblique. Neither of these features is present in the Aldabra material, so they are likely to belong to the remaining Old World scincomorph family, the Scincidae. According to Greer (1970a), only the Lygosominae among the skinks have unpaired frontals.

When the Aldabra material is compared with the lygosomines of the Ethiopian region and the West Indian Ocean, it is apparent that it agrees in detailed structure and proportion only with members of the genus *Mabuya.* This group has perhaps over 100 species distributed through Africa, southern Asia and central and southern America. About 50 of these are found in Africa and nearby islands and of these, 11 occur on islands in the West Indian Ocean including Madagascar. All species of *Mabuya* are generally similar, and many of them also tend to be intraspecifically variable in minor features, so a positive and exhaustive identification of fragmentary material would be extremely time-consuming, or, more probably, impossible. Therefore comparison here is restricted to the species already known from the West Indian Ocean.

Of the seven endemic Madagascan species, *M. gravenhorstii* (Duméril & Bibron, 1839) can be immediately excluded as it has fused frontoparietal scales. *M. elegans* (Peters, 1854) and the closely related *M. sakalava* (Grandidier, 1872) and *M. madagascariensis* Mocquard, 1908 differ from the Aldabra material in their smaller size, very narrow frontal and thin osteodermal layer. Also, the nasal process of the maxilla is more curved in transverse section, and where it forms the anterior lower border of the orbit, the maxilla is reflected outwards, whereas in the Aldabra specimens it is not. With the exception of frontal width, *M. aureopunctata* (Grandidier, 1867) and *M. boettgeri* Boulenger, 1887 also differ from the Aldabra material in these respects. The remaining Madagascar species, the poorly known *M. betsileana* Mocquard, 1906, has not been examined.

Two closely related endemic species of *Mabuya* occur together on the Seychelles : *M. sechellensis* (Duméril & Bibron, 1839), which also reaches the Amirantes, and *M. wrightii* Boulenger, 1887. Both these differ from the Aldabra material in the shape of the maxilla : the anterior portion is more elongate and the upper part of the nasal process is more abruptly turned inwards.

On the Comores, two more species of *Mabuya* occur : the widespread East African *M. striata* (Peters, 1844) on Anjouan and *M. maculilabris* (Gray, 1845) on all the islands of the archipelago. The latter species is found right across tropical Africa. The Comores populations were originally described as a full species, *M. comorensis* (Peters, 1854), but they are now usually regarded as part of the *M. maculilabris* complex and are often considered as a subspecies in which some eastern African populations are also included. *M. striata* differs from the Aldabra material in having the upper edge of the maxilla reflected outwards where it forms the lower border of the orbit. *M. maculilabris*, on the other hand, matches the fossil fragments closely and they fall well within the range of variation encountered in this species. When compared with specimens from Anjouan (BM 77.8.9.1–10, the only Comores material easily available in this study) there is close correspondence in all fragments except the vertebrae. The fossils have the sagittal ridge on the underside of the centrum more marked than the recent specimens. However, at least some *M. maculilabris* from the African mainland (e.g. BM 1970.2134 – Moheli Peninsula, Tanzania ; 1970.2299 – Mombasa) have this feature as well developed as the fossils.

Thus, of the ten West Indian Ocean species of *Mabuya* investigated, the fossils agree best with *M. maculilabris*, which is the one that occurs geographically nearest to Aldabra at the present time.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. The two portions of right maxillae include homologous sections, this is also true of the two dentary fragments. Therefore at least two individuals are represented.

ESTIMATED BODY SIZE. The largest maxilla compares closely with that of a *M. maculilabris* having a head about 20 mm long. This would suggest a snout to vent length of 80 to 95 mm, which is within the present size range of the species.

ORIGIN OF THE POINT HODOUL LIZARD DEPOSIT

The Point Hodoul lizard bones were found in a small solution cavity in the Aldabra limestone. Similar hollows nearby lacked fossil lizards, which might indicate that some factor had concentrated the remains. One possibility is that the cavity, in extended form previous to being reduced to its present size by erosion, acted as a natural trap for lizards. But, if this were so, some lizards might still be expected to occur in similar cavities in the vicinity. Also, the geckoes, which make up a substantial proportion of the fossils, would have been efficient climbers with well developed adhesive toe-pads and it is difficult to envisage any sort of natural pitfall trap from which they would be unable to escape. Another possibility is that the remains represent the food residue of some predator. Such situations are known in the West Indies, where concentrations of the remains of small vertebrates in limestone caves and fissures have often been attributed to predation by owls (Anthony, 1919; Miller, 1929; Hecht, 1951; Etheridge, 1964, 1965, 1966). In these cases, there is sometimes strong circumstantial evidence in the form of associated owl bones (e.g. Wetmore, 1922; Etheridge, 1965 for Hispaniola: Etheridge, 1966 for New Providence). Furthermore, modern deposits of barn owl pellets in the West Indies frequently contain lizard remains (Wetmore & Swales, 1931; Hecht, 1951; Etheridge, 1965) and the kinds of lizards comprising these may occur in similar proportions to those found in some of the fossil deposits.

No owl bones, or those of any other obvious predator, were found in association with the Point Hodoul lizards but, in addition to their concentration, two other factors suggest that such an agent may have produced the deposit. Firstly, the sample shows a bias in the size of the lizards that constitute it, both very large and very small individuals being rare. The great majority have estimated snout to vent lengths of about 40 mm to 100 mm, only two individuals out of 57 (i.e. 3·5%) falling outside this range (see Table 1). Yet the single *Oplurus* in the sample shows that lizards growing to over 200 mm were present on the island and extrapolation from modern forms suggests that lizards much smaller than 40 mm were at least sometimes abundant, since hatchlings of most of the species would have been well below this size (approximate hatching sizes of some modern forms related to the Point Hodoul lizards are as follows: *Geckolepis maculata*, 23 mm – Blanc, 1966; *Paroedura spp.*, 25 mm; *Mabuya maculilabris*, 25 mm). *A priori*, if the deposit represented a natural trap, a predominance of young lizards might be expected as these often wander much more than older animals, yet nearly all the remains are apparently from half-grown or adult individuals. It could be argued that paucity of very small lizards in the sample is due to greater fragility of their remains. This may be so, but at least some elements of the smaller animals present in the deposit are not much more fragmented than those of larger individuals, so the size distribution may not be artificial.

Secondly, a high proportion of the components of the deposit seem to represent nocturnal lizards. Modern *Paroedura* and *Geckolepis* are active at night or are crepuscular whereas *Oplurus*, *Mabuya* and *Phelsuma* (if it was indeed present) are all basically diurnal. Nothing is known about the times of activity of '*Scelotes*' *johannae* and '*S.*' *valhallae*, apparently the closest forms to the Aldabra '*Scelotes*' population, although they too may be at least partly nocturnal. Many tropical and subtropical skinks are night-active and Mertens (1955) states that '*Scelotes*' *splendidus* (Grandidier, 1872) of Madagascar, which is quite similar to '*S.*' *johannae* and '*S.*' *valhallae*, is strictly nocturnal in captivity. If '*Scelotes*' is excluded, the ratio of nocturnal to diurnal individuals is 34 : 4 (89·5%), if it is counted as nocturnal the ratio is 53 : 4

Table 1

Rough estimates of length (snout to vent) of individual lizards in the Point Hodoul deposit

Length (mm snout to vent)	30	40–50	51–60	61–80	81–100	100+	Basis for estimates
Paroedura	1	15	12				Frontals
Geckolepis			1		5		Humeri
? *Phelsuma*		1					Mandible
Oplurus						1	Maxilla and vertebrae
'*Scelotes*'				7	12		Mandibles
Mabuya					2		Maxillae
Number of individuals in each size class	1	16	13	7	19	1	Total = 57

As '*Scelotes*' is much more slender than the other forms, a distribution based on weight rather than length would probably be more or less unimodal.

(93·0% nocturnal) and even if it is regarded as diurnal, nocturnal forms still predominate 34 : 23 (59·7% nocturnal).

Limited size distribution and a high proportion of nocturnal animals would fit predation by an owl. In fact, apart from the single large *Oplurus* and the one juvenile *Paroedura*, both of which may not necessarily have been part of a predator food residue concentration, the size distribution of the Point Hodoul lizards is well within the limits recorded for West Indian owl deposits. While no owls are known from the fossil fauna of Aldabra and none are present now, the cosmopolitan barn owl, *Tyto alba* (Scopoli), was in residence there in 1906 (Benson & Penny, 1971). This species occurs on many quite isolated islands throughout much of the world and is thought to have been one of the agents that produced the West Indian deposits, so it might have produced the Aldabra concentration although some other species could have been responsible.

COMPARISON OF ALDABRA REPTILES WITH THOSE OF NEIGHBOURING AREAS

It is not possible to compare the extinct Aldabra reptiles with even roughly contemporaneous faunas in nearby areas for, with the exception of relatively late material from the Mascarenes, very few Quaternary reptile remains, especially those of lizards, are known from these regions. Table 2 shows the known Aldabra reptile fauna, past and present, and its distribution in neighbouring areas. It is apparent from this that Aldabra has more similarity to Madagascar and the Comores than to mainland East Africa and the Seychelles.

The Comores are thus the island group that shows most resemblance in its present fauna to the Point Hodoul fossil assemblage, which is not unexpected as this archipelago lies less than 400 km from Aldabra. However, the Comores have a number of forms that are unrepresented in the fossil material or indeed in the extant fauna of the atoll. Thus, there are up to three species of *Phelsuma* on each island and on one or more of them occurs the small gecko, *Ebanavia inunguis* Boettger, 1878, chameleons, the skink, *Mabuya striata*, and up to three species of snake. It cannot be ruled out that some of these forms were present on Aldabra when the Point Hodoul deposits were being laid down, for the sample of fossil lizards is very likely not to be fully representative. It is small, consisting of a minimum of 57 individuals, and of the six species present three could be represented by only one, one and two individuals respectively. Even assuming that the remains were randomly accumulated, sampling error alone might have excluded some species. In fact, random accumulation is most improbable, for even a wide-ranging predator is unlikely to have hunted evenly over all habitats of the atoll and, as has been shown, small forms and diurnal ones are under-represented. So, if minute lizards like *Ebanavia* and diurnal forms like chameleons and additional species of *Phelsuma* were present, they might well have been excluded from the sample. For the same reasons, the possibility cannot be discounted that the tiny diurnal skink, *Cryptoblepharus boutoni*, now on the atoll may have been present when the Point Hodoul deposit was formed. The extant gecko, *Hemidactylus mercatorius* Gray, 1842, on

TABLE 2

The known Aldabra reptile fauna and its distribution in neighbouring areas

	Aldabra	Comores	Madagascar	Seychelles	Mainland E. Africa
Geochelone (*Aldabrachelys*)	*	+?	+	+	
Crocodylus niloticus	+	*	*	+	*
Paroedura	+	*	*		
Geckolepis maculata etc.	+	*	*		
Phelsuma	+?/*	*	*	*	
Hemidactylus mercatorius	*	*	*	*	*
Oplurus cuvieri etc.	+	*	*		
'*Scelotes*' *johannae* etc.	+	*	*		
Mabuya maculilabris etc.	+	*	other *Mabuya* spp.	other *Mabuya* spp.	*
Cryptoblepharus boutonii	*	*	*	*	*

* – present. + – known to have occurred in the Quaternary but extinct now. ? – occurrence uncertain.

the other hand is about the same size as the well represented fossil *Paroedura*, probably occupies similar habitats and, like this species, is basically nocturnal, so its absence from the deposit might indicate that it was not on Aldabra when this was laid down.

HABITAT REQUIREMENTS OF EXTINCT ALDABRA REPTILES

Speculating about past vegetation and climate on the basis of the ecological requirements of modern forms that are represented in fossil deposits is a hazardous exercise. This is especially true in the present case, for some of the fossil populations were rather different from the most similar extant forms and it is impossible to be certain that their requirements would have been the same, especially as reptiles colonizing small islands often seem to survive in rather different conditions from those in which their parent populations lived. Such speculation is made more difficult because very little is still known about the basic ecological needs of most West Indian Ocean reptiles. The relevant information that can be assembled is summarized below:

1. Giant tortoises. Recent giant tortoises of the West Indian Ocean, *Geochelone* (sub-genera *Aldabrachelys*, and *Cylindraspis*) have occurred within historical times both on relatively dry, low islands like Aldabra and on better watered, higher ones like Mahé, Mauritius and Rodriguez. It seems likely, therefore, that they are tolerant of a fairly wide range of conditions.

2. *Crocodylus niloticus*. Although most populations live in fresh water, this species can survive in coastal mangrove associations, as it does on parts of the East African seaboard. However, it does not usually occur on bare sea beaches.

3. *Paroedura stumpffi* group. Very little is known about the requirements of any *Paroedura* species, although they normally seem to occur in rather dry habitats and are apparently not closely associated with trees. Virtually nothing appears to have been written about the ecology of *P. sanctijohannis* or *P. stumpffi*. The type of *P. homalorhina* was collected at the entrance to a cave (Angel, 1936), but *P. androyensis*, *P. picta* and *P. bastardi* are recorded from rocky surfaces near the sea (Angel, 1942) and the latter species is also found in semidesert 'brushwood' areas (Angel, 1942; field notes by C. J. Inchley attached to BM 1967.55–67). Blanc & Blanc (1967) also found this species under slabs on rock pavements in deforested mountain areas.

4. *Geckolepis*. The members of this genus seem often to live on the trunks of trees. Angel (1942) records *G. maculata* from crevices in tree trunks and Blanc (1966) found it with *G. typica* in stands of trees with epiphyte-covered boles.

5. *Oplurus cuvieri*. This species is said by Angel (1942) to occur in 'steppe' country in dry places but, as he says that it may be seen on the trunks of trees, it seems probable that it is not confined to really arid areas.

6. '*Scelotes*' nr. *johannae*. Madagascan '*Scelotes*', although all superficially similar in form and all probably basically ground dwelling and rather cryptic, appear to be very varied in their habitat. Thus, some like '*S*.' *igneocaudatus* (Grandidier, 1867)

may be found in semidesert (Angel, 1942), while others, e.g. '*S*' *astrolabi* (Duméril & Bibron, 1839) and '*S.*' *gastrostictus* (O'Shaughnessy, 1879) are partly aquatic (Millot, 1951; Paulian, 1953). Nothing much is known about '*S.*' *johannae*. The types were taken under stones in a sugar plantation on the well vegetated island of Anjouan (Günther, 1880) and another specimen from Moheli (BM 1975.2072) was collected 'under leaf litter of *Terminalia*' by J. Frazier.

7. *Mabuya maculilabris*. Loveridge (1957) states that the East African populations that he refers to *M. m. comorensis* are confined to 'chiefly virgin forest or recently deforested areas' of Kenya and Tanzania. In other regions of mainland Africa, the species apparently occurs in both forest and savannah. On Europa island, it is mainly ground-dwelling but sometimes climbs on tree boles (Brygoo, 1966) and on Moheli, in the Comores, it is often associated with coconut palms, which it may climb to the crown (A. Cheke – personal communication).

It is impossible to gain much idea from the reptile remains of the conditions obtaining when the Bassin Cabri Calcarenites were laid down. Only three species are known from these deposits and of these, one is tolerant of a wide range of conditions (*Geochelone*) and the precise ecological requirements of another (*Oplurus*) are not really known. All that can be said is that the presence of *Crocodylus* suggests that mangroves may have been present near Bassin Cabri at this time.

The fact that the reptiles in the Point Hodoul cavity fillings are like the present Comores fauna may indicate that the deposits were produced at a time when conditions were like those now occurring in that archipelago, which has a higher rainfall and more abundant vegetation than Aldabra. This is supported to some extent by the known habits of *Geckolepis maculata* and *Mabuya maculilabris*, both of which seem to be often associated with large trees; these are not abundant on Aldabra today. The presence of *Crocodylus* at Point Hodoul may indicate that mangrove then occurred on the outer (seaward) edge of the atoll where it is now absent.

POSSIBLE RESOURCE PARTITION BY EXTINCT ALDABRA REPTILES

The six genera of lizards in the Point Hodoul deposit occur together at the present time on Madagascar and on the high, medium-sized island of Grande Comore,* but they are not now found on any small, low island like Aldabra. As both Madagascar and Grande Comore support a wider range of environments than Aldabra ever could, the possibility is raised that the six forms might not have occurred exactly simultaneously on Aldabra. It is therefore worth enquiring whether any of them are so similar in their salient ecological parameters that occupation of quite separate habitats would be necessary to avoid severe competition.

Sympatric lizard species usually partition the resources of their environment on the following bases: temporal separation, differences in habitat or microhabitat, active selection of different sizes of prey and, more rarely, selection of different food *types*. In warm areas, the most obvious temporal separation is into diurnal and

---

* The other Comores islands have five of the genera, but lack *Oplurus*. Blanc (1972) indicates that they all lack *Geckolepis* too and that Grande Comore has no *Paroedura*, but this seems to be erroneous for the Musée Nationale d'Histoire Naturelle, Paris, has a specimen of *Geckolepis maculata* from Mayotte (PM 87.26) and seven *Paroedura sanctijohannis* from Grande Comore (PM 90.14–20).

TABLE 3

Point Hodoul lizard fauna : likely differences in ecologically important parameters

	Probable main period of activity	Approx. maximum head length (mm)	Likely diet	Probable climbing ability	Probable habitat
Paroedura	night	20	invertebrates	good	not typically on trees
Geckolepis	night	27	invertebrates	very good	often on tree boles
'Scelotes'	uncertain	15	invertebrates	very poor	ground-dwelling, probably cryptic in litter etc.
Phelsuma (if present)	day	13	invertebrates	very good	scansorial on various surfaces
Mabuya	day	20	invertebrates	good	ground, also tree boles
Oplurus	day	60+	small animals and vegetation	good ?	ground, also tree boles

nocturnal forms. Habitat differences are often based on variations in insolation, humidity and substrate (e.g. ground type, whether more or less horizontal or vertical surfaces are preferred and, if the latter, whether they are trees, rock faces etc.). As most lizards are general predators, food size is often a more important parameter in reducing competition than food type, although a minority of species are specialists taking high proportions of, for instance, vegetation, ants or small vertebrates.

As stated, not much information is available about the habits of the modern relatives of the members of the Point Hodoul fauna. But what little there is can be augmented by various means, including examination of stomach contents (for dietary differences), speculation based on their morphology and analogies drawn from related forms. Thus, lizard head length often correlates with the size of prey usually eaten, well developed toe-pads in geckoes typically indicate good climbing ability, and large corneas and vertically slit-shaped pupils suggest at least partial nocturnality. Potentially important differences between the Point Hodoul lizards are given in Table 3. From this it can be seen that members of any pair of species may well have differed in at least one parameter of probable ecological significance and usually in more. So, it is unlikely that any of them would have been precise ecological equivalents and there is no reason to think that they could not have coexisted, assuming of course that the atoll supported the minimum microhabitat diversity to allow this.

BODY SIZE AND 'ISLAND GIGANTISM'

The most striking differences between the Point Hodoul lizards and their modern relatives are in apparent maximum size. Thus the linear dimensions of the *Oplurus* may have been almost twice those of the largest living member of the genus and the *Geckolepis* was about 30% longer than the largest species alive today. The *Paroedura* and '*Scelotes*', on the other hand, may have been somewhat smaller than their extant relatives.

A general tendency to large body size in a number of lizard and other groups on small islands is often given formal recognition in the literature as 'island gigantism'. Certainly, in many of the more important lizard families some of the largest forms (although not all) occur on small islands. This is true for geckoes, iguanids, lacertids, skinks and varanids and a similar trend is apparent in land tortoises. One probable reason for this is that many reptiles are much better transmarine colonizers than most mammals and are better at surviving transient periods of adverse conditions. Consequently they often get to, and persist on, small islands where the relatively large mammals that would normally occupy predator and vegetarian niches in mainland areas are entirely absent. The reptiles can therefore expand into this vacant ecological space with consequent increase in body size (or if they were large to start with, without reduction). Very large lizards occur, or have quite recently occurred, on at least five islands or island groups in the African region (see Table 4). Significantly, four out of the five giant forms involved are, or were probably, substantially vegetarian (viz. *Gallotia*, *Macroscincus*, *Phelsuma gigas* and, by analogy with its living relatives, the Aldabra *Oplurus* ; the diet of *Didosaurus* is uncertain).

TABLE 4

Giant lizards on small islands in the African region

Island	Giant form	Family	Maximum size, snout to vent (mm)	Largest related forms in possible source area, or on nearby mainland or large island	Maximum size, snout to vent (mm)	Other forms on same island
W. Canaries	*Gallotia* (*G. goliath*,† *G. simonyi* etc.)	Lacertidae	400+ estimated	*Lacerta lepida* (S.W. Europe, N.W. Africa)	210	Geckoes (*Tarentola*) Skinks (*Chalcides*)
Ilheo Branco and I. Razo, Cape Verde Is	*Macroscincus coctei* (apparently a huge *Mabuya* – see e.g. Greer, in press)	Scincidae	320	*Mabuya perrotetii* (West Africa)	150	Geckoes (*Tarentola*) Skinks (*Mabuya*)
Aldabra	*Oplurus* sp.†	Iguanidae	210–250+ estimated	*Oplurus cuvieri* (Madagascar and Comores)	132	Geckoes (see text) Skinks (see text)
Mauritius	*Didosaurus mauritianus*†	Scincidae	300 estimated	Members of Group II of the *Leiolopisma* assemblage (Greer, 1974) (East Indies)	80*	Geckoes (e.g. *Phelsuma*) Skinks (e.g. *Gongylomorphus*)
Rodriguez	*Phelsuma gigas*†	Gekkonidae	220 estimated	*P. madagascariensis* (Madagascar etc.)	120	Geckoes (e.g. *Phelsuma*)

* but up to 288 mm on some small islands.
† extinct species.

Yet, although this habit is not uncommon in iguanids, it is not, or only weakly, developed in mainland geckoes, skinks and lacertids.

It is also noteworthy that none of the five giants in Table 4 are closely related to each other, even when they occur on neighbouring islands that were probably colonized from the same general source area as with Mauritius and Rodriguez. This indicates that the ability to produce giants is widespread amongst lizards, but possibly once a large form has developed on a small island, its presence inhibits the development of further giants. This is supported by the fact that, in the listed examples, other species coexist with the giants but have not become large, even when they are members of groups that have produced giants elsewhere (the *Mabuya* stock including *Macroscincus, Phelsuma*).

Evolution and maintenance of size differences seem to be common phenomena in island lizards, for instance Schoener (1970) found that *Anolis* (Iguanidae) species in the West Indies often diverge in body size when sympatric. Such differences may be particularly marked on small islands because restricted habitat diversity limits the extent to which species can partition resources by the selection of different microhabitats and therefore increases the need to evolve differences in prey size and hence body size. The large apparent size difference between the two probably nocturnal geckoes in the Point Hodoul cavity filling may be a case in point. Here, *Paroedura* seems to have grown to about 60 mm snout to vent, while *Geckolepis* attained 90 to 100 mm. On the Comores and on Madagascar, members of these two genera do occur together with wide overlap of size, but it is certain that these localities provide a wider range of environments than Aldabra did, so evolution of clear size differences has not been necessary.

As might be expected from experience with domestic animals, size in vertebrates is often very labile and easily modified by selection. Certainly in lizards the body size of populations may vary quite extensively through time. For instance Etheridge (1964, 1965, 1966) found that in the West Indies the body size of several species was considerably less than that of presumed ancestral fossil populations on the same island.

POSSIBLE CAUSES OF EXTINCTION

Although one cannot be sure that none of the present lizards of Aldabra was on the atoll when the Bassin Cabri Calcarenites and the Point Hodoul deposits were formed, it is certain that the crocodile and the six lizards represented in them are now extinct on the island. Among possible reasons for their disappearance are: (1) competitive exclusion by forms now present on the island; (2) extermination by an invading predator; and (3) transient or permanent loss of essential ecological resources.

Competitive exclusion

If the three present Aldabra lizards arrived after the Point Hodoul deposit was formed, it is possible that they could have displaced some of the species represented in it. However, in a stable situation, with no accompanying changes in ecological resources, this would only be likely to happen if the ecological space required by the invader more or less completely overlapped that of one or more of the species already there. Also, in a stable situation, an island lizard is quite likely to be better adapted to its immediate environment than one coming from elsewhere. This, together with the fact that an invader would be initially greatly outnumbered and would just have completed a debilitating transmarine journey, should give the original inhabitant great advantages over potential competitors arriving from outside. If, on the other hand, the island environment was undergoing change at the time of invasion in a way that favoured the incursor, then replacement would be more likely.

It is possible that *Hemidactylus mercatorius* has roughly the same requirements as the Aldabra *Paroedura* (see p. 104) and *Phelsuma abbotti* might be the ecological equivalent of the putative *Phelsuma* in the Point Hodoul deposits. The third species now on Aldabra, the skink *Cryptoblepharus boutonii*, is too small to have been a competitor of either of the fossil skinks, unless of course it competed with their young. But this is not very likely, especially as it is known that *Cryptoblepharus* can coexist on small islands with forms identical with, or very similar to, the fossils: it occurs with *Mabuya maculilabris* on Europa and with *'Scelotes' valhallae* on Glorioso. So, the present species would only have been likely to displace at most two of the six Point Hodoul lizards.

Extermination by an invading predator

On small islands, introduced predators often destroy a high proportion of indigenous reptiles. Mongooses and rats were probably responsible for the extermination of many endemic West Indian populations and a similar process seems to have taken place on Rodriguez and Mauritius, the former island having lost its two native geckoes. Ten endemic Mascarene reptile species probably occurred on Mauritius of which six are no longer found on the main island and a seventh is apparently restricted to a single locality there (for the lizards, see Vinson & Vinson, 1969, and Vinson, 1973). Habitat destruction may have contributed, but it does not seem to have been the main factor, for five of the forms now extinct on Mauritius itself still survive on offshore islands that are free of mammalian predators even though the natural vegetation is greatly reduced. In such cases, the predators concerned are ones with a broad dietary tolerance, so that a fall in numbers of a particular prey-type does not produce a corresponding drop in predator numbers through starvation. Consequently, predator pressure on a declining species is not reduced. Presumably, island endemics are exterminated because they lack the requisite antipredator strategies to resist an invader and, as the numbers of individuals and their range is restricted, they are hunted out swiftly, before these can evolve.

One can envisage a natural situation like this with perhaps an avian predator arriving on an isolated small island like Aldabra. As has been suggested, owls may have been active when the Point Hodoul deposit was formed and rats have reached the island since (presumably by human agency). Both of these might have been capable of reducing the fauna, but it is very difficult to assess their actual importance.

Loss of ecological resources

It is likely that the number of forms an island can support is partly dependent on habitat diversity. Reduction in diversity, even transiently, may mean that some species would not survive. Such reduction may have occurred on Aldabra. For instance, the presence of *Geckolepis* and *Mabuya* nr. *maculilabris* in the Point Hodoul deposit suggests that large trees may have been more abundant at this time ; reduction or temporary complete loss of these could have hazarded the lizards. However, it is not easy to see why so many of the fossil forms disappeared. One possibility is that the island suffered a transient period of very adverse conditions, for instance an extended drought. Such an event seems quite possible in the varying climatic conditions of the late Quaternary. A low atoll like Aldabra would be more prone to extreme drought than high islands like the Comores where orographic influences probably produced a more stable rainfall. These islands still possess a fauna similar to that represented in the Point Hodoul deposits. In the West Indian Ocean, low islands certainly seem more prone to extinction of their faunas, for their level of endemicity is much lower than that on high islands (Peake, 1971). Braithwaite *et al.* (1973) suggest that the breaching of the Aldabra land rim and the flooding of the lagoon, which took place perhaps 4000 to 5000 years ago and reduced the area of the island by 60%, may have been responsible for widespread destruction of habitat and consequent extermination. Whether one or both these factors were responsible, permanent or transient loss of ecological resources seems a likely primary cause of the extinction of the Point Hodoul reptile fauna. Even if competitive replacement was also involved it would have been most likely to take place in such a changing environment.

COLONIZING ABILITY OF ALDABRA REPTILES

It is virtually certain that Aldabra received its reptiles by transmarine migration (although one or more of the modern species might possibly have been transported by man), so one would expect the forms that reached the atoll to have been well adapted to the hazards of sea crossings and the perilous early stages of colonization. There is some circumstantial evidence that this is so. One indication is that all the reptile groups known from Aldabra have got to at least one other oceanic island that would have required a transmarine journey. *Paroedura*, *Geckolepis* and *Oplurus* are all on the Comores, *Mabuya* and *Crocodylus* reached this archipelago and the Seychelles as well, and the other groups (if '*Scelotes*' is taken to include the endemic scincines of Mauritius and the Seychelles) got to a relatively large number of islands in the West Indian Ocean.

Aldabra has probably been completely submerged twice during its occupation by giant tortoises, which would imply that they colonized the atoll not once but three times (Braithwaite *et al.*, 1973). Similarly, remains of *Crocodylus* and *Oplurus* occur in both the Bassin Cabri Calcarenites and the Point Hodoul cavity fillings. These deposits are separated by the marine Aldabra limestone, so the reptiles common to them must have colonized at least twice.

In the West Indies, the species of the iguanid genus *Anolis* that are successful colonizers are all typical of savannah or open forest situations, none of them being mainly rain forest or montane forms (Williams, 1969). Wilson (1959, 1961) has found an analogous situation in Melanesian ants. With the exception of the crocodile, the reptiles that have reached Aldabra fit this pattern. All those in which habits are known or can be guessed would be expected to occur at least sometimes in fairly dry habitats, such as littoral situations (in the case of *Cryptoblepharus*) or savannah. This is true even of the probably tree-associated forms, *Geckolepis* and *Mabuya* nr. *maculilabris*. Williams thinks that this general trend results from the greater ability of dry-adapted animals to survive the almost inevitable desiccation of a sea passage.

Another characteristic to be expected in successful colonizers is the ability to swim, or float, or cling to rafting vegetation. *Crocodylus niloticus* sometimes lives permanently in coastal areas and is obviously well fitted for survival at sea, and giant tortoises are known to float well (see e.g. Grubb, 1971). Virtually all the Aldabra lizards have, or had, good climbing ability and consequently might be expected to maintain their position well on floating objects. The only exception is the very short-legged, probably ground-dwelling '*Scelotes*'.

Parthenogenesis is obviously an initial advantage in a colonizing species since any individual of an all-female species, irrespective of age, can form a propagule. Some of the most widespread species of oceanic reptiles seem to be parthenogenetic including the worm snake, *Ramphotyphlops braminus* (Daudin, 1803) – McDowell, 1974, and the gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836) – Gorman, 1973, but all four reptile species on Aldabra at the present time are bisexual and none of the fossil forms belong to genera in which parthenogenesis has been reported.

ACKNOWLEDGEMENTS

Special thanks are due to the Royal Society who enabled the material on which this paper is based to be collected and made it available to me. I should also like to acknowledge the considerable help given to me by various individuals, in particular that of Dr J. D. Taylor who collected the specimens. Mr C. J. McCarthy made skeletons and radiographs of comparative material and the fossils were prepared by Mr F. M. P. Howie and Mr N. Hughes. Fig. 3 was drawn by Dr A. W. H. Bartram. Professor J. Guibé (Muséum Nationale d'Histoire Naturelle, Paris) arranged the loan of some critical specimens from Madagascar and the Comores in his care. The manuscript was read by Miss A. G. C. Grandison, Mr J. F. Peake and Dr Taylor, all of whom provided helpful criticism.

REFERENCES

ANGEL, F. 1936. Deux gekkos nouveaux de Madagascar appartenant au genre *Phyllodactylus*. *Bull. Soc. zool. Fr.* **61** : 508–511.

—— 1942. Les lézards de Madagascar. *Mem. Acad. malagache*, **36** : 1–193.

ANTHONY, H. E. 1919. Mammals collected in eastern Cuba in 1917, with descriptions of two new species. *Bull. Am. Mus. nat. Hist.* **41** : 625–643.

BELLAIRS, A. D'A. 1969. *The life of reptiles, vol. II*. London.

BENSON, C. W. & PENNY, M. J. 1971. The land birds of Aldabra. *Phil. Trans. R. Soc. B.* **260** : 417–527.

BLANC, C. P. 1966. Notes sur les Gekkonidae de Madagascar : I – Observations relatives à deux espèces de *Geckolepis* : *G. maculata* Peters, 1880 et *G. typica* Grandidier, 1867. *Vie Milieu*, **17** : 453–460.

—— 1972. Les reptiles de Madagascar et des îles voisines. *In* Battistini, R. & Richard-Vindard, G. (eds), *Biogeography and ecology in Madagascar* : 501–614. The Hague.

—— & BLANC, C. F. 1967. Observations écologiques sur les Sauriens du Mont Bity. *Ann. Univ. Madag.* (*Série Sci. Nat. Mat.*), **5** : 67–74.

BRAITHWAITE, C. J. R., TAYLOR, J. D. & KENNEDY, W. J. 1973. The evolution of an atoll : the depositional and erosional history of Aldabra. *Phil. Trans. R. Soc. B*, **266** : 307–340.

BRAVO, T. 1953. *Lacerta maxima* n. sp. de la fauna extinguida en el Pleistoceno de las Islas Canarias. *Estudios geol. Inst. Invest. geol. Lucas Mallada*, **9** : 7–34.

BRYGOO, E. R. 1966. Note sur les reptiles terrestres récoltés à Europa en Avril 1964. *Mem. Mus. natn. Hist. nat. Paris* (*Série A*), **41** : 29–31.

COTT, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29** (4) : 211–350.

DIXON, J. R. & KROLL, J. C. 1974. Resurrection of the generic name *Paroedura* for the phyllodactyline geckoes of Madagascar, and a description of a new species. *Copeia*, **1974** (1) : 24–30.

ETHERIDGE, R. 1964. Late Pleistocene lizards from Barbuda, British West Indies. *Bull. Fla St. Mus. biol. Sci.* **9** (2) : 43–75.

—— 1965. Fossil lizards from the Dominican Republic. *Q. Jl Fla Acad. Sci.* **28** (1) : 83–105.

—— 1966. Pleistocene lizards from New Providence. *Q. Jl Fla Acad. Sci.* **28** (4) : 349–358.

GORMAN, G. C. 1973. The chromosomes of the Reptilia, a cytotaxonomic interpretation. *In* Chiarelli, A. B. & Capanna, E. (eds), *Cytotaxonomy and vertebrate evolution* : 349–424.

GREER, A. E. 1970a. A subfamilial classification of scincid lizards. *Bull. Mus. comp. Zool. Harv.* **139** (3) : 151–183.

—— 1970b. The systematics and evolution of the subsaharan Africa, Seychelles and Mauritius scincine scincid lizards. *Bull. Mus. comp. Zool. Harv.* **140** (1) : 1–23.

—— 1974. The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. *Aust. J. Zool.* Supplementary series **31** : 1–67.

—— (in press). On the evolution of the giant Cape Verdes scincid lizard *Macroscincus coctei*. *J. nat. Hist.*

GRUBB, P. 1971. The growth, ecology and population structure of giant tortoises on Aldabra. *Phil. Trans. R. Soc. B.* **260** : 327–372.

GÜNTHER, A. 1879. On mammals and reptiles from Johanna, Comoro Islands. *Ann. Mag. nat. Hist.* (5) **3** : 215–219.

—— 1880. Description of new species of reptiles from Eastern Africa. *Ann. Mag. nat. Hist.* (5) **6** : 234–238.

HECHT, M. K. 1951. Fossil lizards of the West Indian genus *Aristelliger* (Gekkonidae). *Am. Mus. Novit.* **1538** : 1–33.

LOVERIDGE, A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda ; Kenya ; Tanganyika ; Zanzibar). *Bull. Mus. comp. Zool. Harv.* **117** (2) : 153–362.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography*. Princeton, New Jersey.

McDOWELL, S. B. 1974. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum, part I. Scolecophidia. *J. Herpetol.* **8** (1) : 1–57.

MERTENS, R. 1955. Studien über die Reptilienfauna Madagaskars, I. Beobachtungen an einigen madagassischen Reptilien im Leben. *Zool. Gart. Lpz.* **22** : 57–73.

MILLER, G. S. 1929. A second collection of mammals from caves near St. Michel, Haiti. *Smithson. misc. Colls*, **74** (3) : 1–8.

MILLOT, J. 1951. Un lézard d'eau à Madagascar (*Scelotes astrolabi* Dum. et Bib.). *Naturaliste malagache*, **3** : 87–90.

OELRICH, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Publs Mus. Zool. Univ. Mich.* **94** : 1–122.

PAULIAN, R. 1953. A propos des lézards aquatiques. *Naturaliste malagache*, **5** : 108.

PEAKE, J. F. 1971. The evolution of terrestrial faunas in the Western Indian Ocean. *Phil. Trans. R. Soc. B*, **260** : 581–610.

SAVAGE, J. 1952. The correct generic names for the iguanid lizards of Madagascar and the Fiji islands. *Copeia*, **1952** (3) : 182.

SCHOENER, T. W. 1970. Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species – displacement and convergence. *Am. Nat.* **104** : 155–173.

THOMPSON, J. & WALTON, A. 1972. Redetermination in the chronology of Aldabra Atoll by ^{230}Th/^{234}U dating. *Nature, Lond.* **240** : 145–146.

VINSON, J. & VINSON, J.-M. 1969. The saurian fauna of the Mascarene Islands. *Bull. Mauritius Inst.* **6** (4) : 203–320.

VINSON, J.-M. 1973. A new skink of the genus *Gongylomorphus* from the Macabé Forest (Mauritius). *Revue agric. sucr. Île Maurice*, **52** : 39–40.

WETMORE, A. 1922. Remains of birds from caves in the Republic of Haiti. *Smithson. misc. Collns*, **74** (4) : 1–4.

—— & SWALES, B. H. 1931. The birds of Haiti and the Dominican Republic. *Bull. U.S. natn. Mus.* **155** : 234–236.

WILLIAMS, E. E. 1969. The ecology of colonisation as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* **44** (4) : 345–389.

WILSON, E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. *Evolution, Lancaster, Pa*, **13** : 122–144.

—— 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* **95** : 169–193.

E. N. ARNOLD D. Phil.
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. Kay, E. Alison. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.)
2. Whitehead, P. J. P. The Clupeoid Fishes described by Lacepède, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. Taylor, J. D., Kennedy, W. J. & Hall, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates 77 Text-figures. 1969. £4.50.
4. Haynes, J. R. Cardigan Bay Recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. Pp. 245; 33 Plates, 47 Text-figures. 1973. £10.80.
5. Whitehead, P. J. P. The Clupeoid Fishes of the Guianas. Pp. 227; 72 Text-figures. 1973. £9.70.
6. Greenwood, P. H. The Cichlid Fishes of Lake Victoria, East Africa: the Biology and Evolution of a Species Flock. Pp. 134; 1 Plate, 77 Text-figures. 1974. £3·75.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

A REVIEW OF THE FAMILY CANIDAE, WITH A CLASSIFICATION BY NUMERICAL METHODS

B. M. S. MUSEUM
GENERAL
21 APR 1976
LIBRARY
NATURAL HISTORY

J. CLUTTON-BROCK, G. B. CORBET & M. HILLS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 3
LONDON : 1976

A REVIEW OF THE FAMILY CANIDAE, WITH A CLASSIFICATION BY NUMERICAL METHODS

BRITISH MUSEUM
GENERAL
21 APR 1976
LIBRARY
NATURAL HISTORY

BY

JULIET CLUTTON-BROCK, GORDON B. CORBET
& MICHAEL HILLS

Pp 117–199; 11 *Text-figures,* 9 *Tables*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 3
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 29 *No.* 3 *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

ISSN 0007-1498

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 13 *April*, 1976 *Price* £5·95

A REVIEW OF THE FAMILY CANIDAE, WITH A CLASSIFICATION BY NUMERICAL METHODS

By JULIET CLUTTON-BROCK, G. B. CORBET & M. HILLS

CONTENTS

	Page
Synopsis	119
Introduction	120
Characters of the Canidae	121
Sources of data	123
Selection of species	123
Derivation of data	124
Nature of the data	125
Kinds of characters	125
Use of the data matrix	125
Measurement of similarity	126
Numerical results	126
Distribution of similarity	126
Near neighbours	128
Two-dimensional plots	128
Similarity values for the existing classification	133
Homogeneity of the three main genera	136
Automatic Classification	137
General taxonomic conclusions	139
Systematic account	141
Genus *Canis*	141
Genus *Vulpes*	150
Genus *Alopex*	161
Genus *Otocyon*	162
Genus *Nyctereutes*	164
Genus *Dusicyon*	165
Genus *Chrysocyon*	176
Genus *Speothos*	177
Genus *Cuon*	179
Genus *Lycaon*	180
Acknowledgements	181
Appendix I: Data matrices	182
Appendix II: Lice (Phthiraptera) of the Canidae	194
References	195

SYNOPSIS

Within the accepted classification of the Canidae it is usual to recognize three subfamilies, fourteen genera and thirty-seven species, excluding the domestic dog. Using numerical methods and a total of ninety characters an analysis has been carried out of the overall similarity between thirty-five of these species plus two breeds of domestic dog. The specimens used for this analysis are in the collections of the British Museum (Natural History). Classification above the level of species has been critically examined on phenetic characters. The results demonstrate the isolated positions of the monospecific genera *Lycaon*, *Speothos* and *Cuon* and do not strongly support their grouping as a discrete subfamily. The status of *Otocyon*, *Nyctereutes*, *Chrysocyon* and *Alopex* as monospecific genera is also upheld although *Alopex* is clearly related to the other foxes of the genus *Vulpes*. *Urocyon* and *Fennecus* are included in *Vulpes*, and *Cerdocyon* and *Atelocynus* in *Dusicyon*.

The three larger genera, *Canis*, *Vulpes* and *Dusicyon*, are retained although they are closely interrelated. *Vulpes vulpes* is shown to be a distinctly atypical member of its genus. The position of the extinct Falkland Island wolf was found to be enigmatic but it is provisionally retained with other species of *Dusicyon*.

A systematic description is given of each species and the data are presented as a series of tables that may be used for reference.

INTRODUCTION

The Canidae, comprising the dogs and foxes, is one of the most clear-cut families of mammals and its content has rarely been seriously disputed since Gray (1821, 1825) first used the name in its present form. Exceptions to this unanimity amongst taxonomists have been the proposal to include the bears and the dogs in a single family (Winge, 1924) ; and at the other extreme the splitting of the Canidae by giving family rank to some of its more aberrant members, e.g. the Otocyonidae of Trouessart (1885) for the single species *Otocyon megalotis*, the bat-eared fox. Neither of these courses has received general acceptance.

The relation of the Canidae to other families of carnivores has been rather more controversial. This was discussed in some detail by Simpson (1945) who accepted the grouping of the Canidae with the Ursidae (bears), Procyonidae (racoons etc.) and Mustelidae (weasels etc.) in a superfamily Canoidea (frequently called the Arctoidea in the older literature), contrasting with the superfamily Feloidea (frequently Ailuroidea in the past) containing the Felidae (cats), Viverridae (civets etc.) and Hyaenidae (hyaenas).

In contrast to the stable concept of the family Canidae, classification within the family has been distinctly unstable. At the species level revisionary work has progressively clarified the limits of the separate species until at present the only real uncertainty concerns the South American forms usually placed in the genus *Dusicyon* s.l. Classification at the generic level has been particularly unstable and even those generic allocations that have stood intact for the past century have done so by neglect rather than by the soundness of their foundations. The genus *Cuon* for example, containing the single species *C. alpinus*, the red dog of S.E. Asia, is usually diagnosed in terms of a single character, namely the absence of third lower molars. The Simien jackal of Ethiopia has been variously considered to be the sole member of a genus *Simenia* or has been placed with the other jackals in *Canis*. Likewise the Arctic fox has been given generic rank as *Alopex lagopus* or has been included in *Vulpes*. Although these are to some extent questions of taxonomic rank there has been a tendency to attempt to settle them in isolation without taking into account other members of the genera concerned.

Grouping of the genera into subfamilies has been equally controversial. Simpson (1945) probably followed some degree of consensus in recognizing three subfamilies: Otocyoninae (*Otocyon*), Simocyoninae (*Lycaon, Cuon, Speothos*) and Caninae (all other genera). But these members of the Simocyoninae are so diverse that many doubts have been expressed about the validity of such a grouping.

The last comprehensive revision of the Canidae was that of Mivart (1890) since when an enormous amount of relevant data has accumulated and many piecemeal taxonomic changes have been made. The main objective of the present study was therefore to revise the classification within the family, taking account of all species and all available characters. No attempt was made to resolve outstanding problems at the species level.

The principle followed in determining which characters to use was to include all characters that showed clear-cut interspecific differences anywhere within the family. Most previous studies of classification in mammals using numerical methods have been confined to limited sets of characters, e.g. that of parts of the Felidae by Imaizumi (1967) using only the skull and that of New Guinea rodents by Lidicker (1973) using only the penis. These seem to have the weakness of including many characters that show very little variation within the group concerned and of ignoring major differences in other parts of the body. By using all those characters showing major, clear-cut differences between species, it was hoped that a sufficiently large and representative sample of characters would be obtained without having to include the more subtle differences that can only be detected in terms of differences in mean value between one species and another.

As is the case with most groups of mammals, literature on the Canidae is excessively fragmented. It was therefore considered that the data matrices would in themselves be a useful source of information and they are presented here (Tables 4–9) in a form that we hope will be of value for reference. Recently a comprehensive popular account of the family has been produced by Bueler (1974), and a more technical review, within the framework of behaviour patterns, by Fox (1975).

CHARACTERS OF THE CANIDAE

The Canidae are cursorial, terrestrial carnivores that have their young in burrows or dens in the ground. The family is distributed over the greater part of the habitable world with the exception of some oceanic islands. The species may be solitary, hunting on their own or in restricted family groups and living off small prey, or they may be social pack animals like the wolves that hunt large prey. All canids will feed on some vegetable matter and carrion, especially when the preferred diet is scarce. In all species the jaws are well developed, the head is longer than in the cat family, and the ears are prominent. The body is lightly built and the limbs are long. Pelage characters are variable but the dominant colours are black, white, grey and ochreous or tawny brown. There is usually a dense underfur mixed with longer dark or 'agouti' guard hairs (Little, 1957). The tail is usually bushy, often with a contrasting black or white tip and a patch of dark hairs on the dorsal part covering a glandular area (called the 'tail gland' throughout this work, see

Hildebrand, 1952b). The fur is thicker and lighter coloured in the winter and in low temperature zones. The underparts of the body, inner sides of the limbs and insides of the ears are usually paler in colour than the rest of the body.

The sense organs are well developed and most species are predominantly nocturnal. Individuals communicate with each other by facial expression, body and tail posture and by howling, yelping or barking.

The limbs are long and slender and adapted for swift running. There are four functional digits on each limb. On the fore-limb in all species except *Lycaon pictus* the first digit is vestigial and is represented by a claw and small pad higher up on the foot than the four functional pads. In *L. pictus* this digit is totally absent. In the domestic dog and dingo a vestigial first digit may also be present as a 'dew claw' on the hind limb as well. This may be occasionally observed in wild canids (see, for example, Lönnberg, 1916, for a report of 'dew claws' on a wild fox).

The facial part of the skull in the Canidae is elongated, the zygomatic arches are wide and the bony orbits never form a complete ring. The temporal ridges may be either wide and enclose a lyriform sagittal area or they may be fused to form an interparietal crest. The 'brows', that is, the part of the frontal bones above and between the eyes, may be slightly dished, as in the foxes, flat as in most of the species of *Dusicyon* or convex as in the dog and wolf. The development of the 'brows' is a reflection of the size of the frontal sinuses. The postorbital process of the frontal bone usually ends in a small point. The auditory bulla is relatively large, rounded and divided internally by an incomplete septum.

The dental formula for all species is, $I\,\frac{3}{3}$, $C\,\frac{1}{1}$, $P\,\frac{4}{4}$, $M\,\frac{2}{3}$, with the following exceptions: *Otocyon megalotis* – $I\,\frac{3}{3}$, $C\,\frac{1}{1}$, $P\,\frac{4}{4}$, $M\,\frac{3}{4}$; *Speothos venaticus* – $I\,\frac{3}{3}$, $C\,\frac{1}{1}$, $P\,\frac{4}{4}$, $M\,\frac{1}{2}$; *Cuon alpinus* – $I\,\frac{3}{3}$, $C\,\frac{1}{1}$, $P\,\frac{4}{4}$, $M\,\frac{2}{2}$. In every species except *O. megalotis* P^4 and M_1 (the carnassials) are larger than all the other teeth; they are trenchant and bite together with a shearing action. In *Otocyon*, however, these teeth are molariform and no larger than the rest. In all canids the canine teeth are long and more or less sharply pointed; the premolars are also pointed and have one main cusp. The molars, with the exception of the lower carnassial (M_1), are bunodont. In the majority of species the talonid or heel of the lower carnassial has two cusps, but in *S. venaticus*, *C. alpinus* and *L. pictus* it is crested and has only one cusp. The homologies and development of the cusp patterns in the Canidae were discussed by Marett Tims (1896) but it is a subject that has since received little attention.

In general, the canids being highly cursorial, the family is not found in dense forest areas; three exceptions are *C. alpinus* (Oriental region), *S. venaticus* and *Dusicyon microtis* (both of the Brazilian subregion of South America). All the races of wolf and almost all the species of true fox (genus *Vulpes*) are found in the northern hemisphere. The coyote, *Canis latrans*, of North America is replaced in southern Europe, Africa and the Orient by the several species of jackal. In Africa the ecological niche of the wolf is taken by *L. pictus*, the hunting dog.

SOURCES OF DATA

Selection of species

The 37 species of wild canids are listed below, named and arranged according to what can be considered a consensus of current views on their classification. The arrangement of subfamilies and genera follows Simpson (1945) except that *Cerdocyon* and *Atelocynus* are given generic rank following Cabrera (1958). The species are delimited according to the most recent major regional works, namely those of Ellerman & Morrison-Scott (1966) for the Palaearctic and Oriental regions, Ellerman *et al.* (1953) for southern Africa, Hall & Kelson (1959) for North America and Cabrera (1958) for South America. *Canis simensis*, from Ethiopia, is the only species not included in these and its specific distinctness has never been in doubt. All of these species were used in this study with two exceptions, marked *, of which no specimens were available in the British Museum (Natural History). These are *Urocyon littoralis*, the grey fox from the Santa Barbara Islands, California, treated as specifically distinct from the continental *Urocyon cinereoargenteus* by Hall & Kelson, and *Canis rufus* (= *C. niger*), the red wolf of southeastern U.S.A. Both of these appear to be sufficiently similar to their better known relatives, *U. cinereoargenteus* and *Canis lupus* respectively, that their generic allocations can be presumed to follow those of the larger species.

The generic name *Oreocyon*, replaced by *Dasycyon* (sic), has been proposed for a new species of canid, *Dasycyon hagenbecki*, based on a single skin from the Andes of South America (see Krumbiegel, 1953). The existence of this species has not been corroborated by further finds and we have not included it in this study. In addition to these wild species two forms of domestic dog were included, the dingo of Australia to represent a primitive breed and the bloodhound as an example of a highly differentiated breed.

Present classification of the family Canidae :

Subfamily CANINAE

Canis lupus Wolf	Europe, Asia, N. America, Arctic
Canis rufus Red wolf*	Central N. America
Canis latrans Coyote	N. America
Canis aureus Golden jackal	S.E. Europe, N. Africa, S. Asia
Canis mesomelas Black-backed jackal	Africa south of the Sahara
Canis adustus Side-striped jackal	Africa south of the Sahara
Canis simensis Ethiopian jackal	Mountains of Ethiopia
Alopex lagopus Arctic fox	Arctic
Vulpes vulpes Common or red fox	Europe, N. Africa, Asia, N. America
Vulpes corsac Corsac fox	Central Asia
Vulpes ferrilata Tibetan sand fox	Tibetan plateau
Vulpes bengalensis Bengal fox	India
Vulpes cana Blanford's fox	S.W. Asia
Vulpes rueppelli Sand fox	N. Africa, S.W. Asia
Vulpes pallida Pale fox	Southern edge of Sahara
Vulpes chama Cape fox	S. Africa
Vulpes velox Kit fox	N. America

Fennecus zerda	Fennec fox	N. Africa, Arabia
Urocyon cinereoargenteus	Grey fox	N. America, northern S. America
*Urocyon littoralis**	Island grey fox	Islands off California
Nyctereutes procyonoides	Raccoon dog	E. Asia
Dusicyon australis	Falkland Island wolf	Falkland Is., extinct since *c.* 1880
Dusicyon culpaeus	Colpeo fox	S. America – Patagonian subregion
Dusicyon culpaeolus		Uruguay
Dusicyon gymnocercus	Azara's fox	Eastern Patagonian subregion
Dusicyon inca		Mountains of Peru
Dusicyon griseus	Argentine grey fox	S.W. Patagonian subregion
Dusicyon fulvipes	Chiloe fox	Island of Chiloe
Dusicyon sechurae	Sechura desert fox	N.W. Peru, Ecuador
Dusicyon vetulus	Hoary fox	Brazil
Cerdocyon thous	Common zorro	S. America – Brazilian subregion
Atelocynus microtis	Small-eared zorro	Central S. America – Brazil
Chrysocyon brachyurus	Maned wolf	Southern Brazilian subregion
Subfamily SIMOCYONINAE		
Speothos venaticus	Bush dog	S. America – Brazilian subregion
Cuon alpinus	Dhole	E. and Central Asia
Lycaon pictus	Hunting dog	Africa south of the Sahara
Subfamily OTOCYONINAE		
Otocyon megalotis	Bat-eared fox	Africa south of the Sahara

Derivation of data

The data relating to each species were derived primarily from specimens in the collections of the British Museum (Natural History), supplemented by information from the literature. Whenever possible, three skulls and skeletons of each species were selected and included one male and one female. All measurements were taken with dial calipers. The skeletal measurements are defined in the figures accompanying Tables 4, 5, and 8. A character that has been used in diagnosing the genera of canids is the relative development of the frontal sinuses in the skull. In order that this character could be assessed correctly at least one skull from each genus was sectioned diagonally through the cranium to expose the sinuses.

For characters of the pelage all the skins of most of the species were examined and scoring was done on between 3 and 10 skins. In defining the pelage characters account was taken of the genetics of coat colour as described by Little (1957). Assessments of hair and skin colours were made by eye and estimates of the thickness of the hair were made by rubbing one hair at a time between the thumb and forefinger.

Characters concerning internal anatomy, body proportions of the live animal, and comparative behaviour were extracted from published works and were scored in the same way as the directly measured variables. The sources of these data are given with the descriptions of the characters in Tables 4–9.

NATURE OF THE DATA

Kinds of characters

The list of characters given in Tables 4–9 (p. 182) includes qualitative, quantitative and derived characters.

Qualitative. These are characters whose values are simply alternatives from a list. Comparisons of magnitude between the different values are meaningless.

Quantitative. There are two main types of quantitative character. The first takes values on an ordinal scale for which comparisons of order are possible. For example character 7, Table 7, *dark patch on dorsal surface of tail*, takes the values *absent/short/long* and short is intermediate between absent and long. The second takes values on a scale for which differences and ratios of values may be compared. All the linear measurements on the skull fall into this category.

Derived. These are characters whose values are derived from the actual observations on the specimen. The condylo-basal length of the skull was used as the best available measure of overall size. Since the range of size in the family is very considerable, all other linear measurements were used in the form of ratios, frequently to condylo-basal length. The attempt to eliminate size-dependence by using characters derived as ratios can only be partially successful, but at least the derived characters are measuring aspects of shape which are far less size-related than the original characters.

All the character values were obtained separately for each specimen. For quantitative characters these values usually varied within a species and a value for the species was obtained by averaging the values for the specimens. For characters taking values on an ordinal scale the coded values (such as 1, 2, 3) were averaged. This is not ideal because it presumes that 2 is exactly halfway between 1 and 3 whereas it is only known that 2 is intermediate between 1 and 3. Because the values of these characters did not vary much in this study the difficulty was ignored. The values of qualitative characters showed no variation so the common value was used for the species.

Use of the data matrix

The characters employed have been presented in Tables 4–9 in a form suitable for general-purpose reference. There are, however, limitations on their use that must be stressed. In particular the mean values given for the quantitative characters should not be used for further statistical studies without taking full account of the very small sample size (usually three). In the context of the analysis presented here, using 90 characters, it is thought that the errors inherent in these mean values are not important, especially where the range of values for a given character is great, e.g. condylo-basal length of the skull for which the mean value for a species varies from 82 to 226 mm. It would, however, be quite inappropriate to use these figures as a precise measure of the difference in value between closely similar species, especially in the case of those species such as *Canis lupus* and *Vulpes vulpes* that have enormous ranges and considerable geographical variation. For the same reason elaborate and more accurate methods of measuring characters of the pelage were considered to be inappropriate.

The main value of the data matrix is, we believe, in showing how the characters of a particular species relate to the variation found in the family as a whole, rather than as a basis for the detailed comparison of closely related species.

MEASUREMENT OF SIMILARITY

A measure of similarity between each pair of species was obtained by first allowing both qualitative and quantitative characters to contribute amounts between 0 and 100, and then averaging the contributions over characters. The rules were :

(i) a qualitative character contributed 100 if the two species had the same value and 0 otherwise, regardless of whether the value represented the 'presence' or the 'absence' of something ;

(ii) a quantitative character contributed an amount proportional to the difference in the character value for the two species ; the proportion was chosen so that the largest difference between any pair of species in the study contributed 100 and a zero difference contributed 0 ;

(iii) if a character was recorded as missing on a species because its value was not known then that character was ignored when assessing similarity of all other species with that species.

This way of measuring similarity is the method used in the CLASP package of programs for numerical taxonomy (Rothamstead Experimental Station) and has been discussed in detail by Gower (1971). A number of minor variations in the method are included in the package.

All analyses of similarity values were carried out twice : once using all the characters listed in Tables 4–9 (referred to as 'All characters') and again using only characters of the skull and teeth (Tables 4 and 5), these being the characters that traditionally have been given greatest weight in mammalian classification.

NUMERICAL RESULTS

Distribution of similarity

The result of the process of selecting characters, observing their values and measuring similarity is a set of similarities on a scale 0–100 consisting of one for each pair of species. In this study there were 37 species and 666 similarities. Frequency distributions of similarities are shown in Fig. 1 and indicate the range of

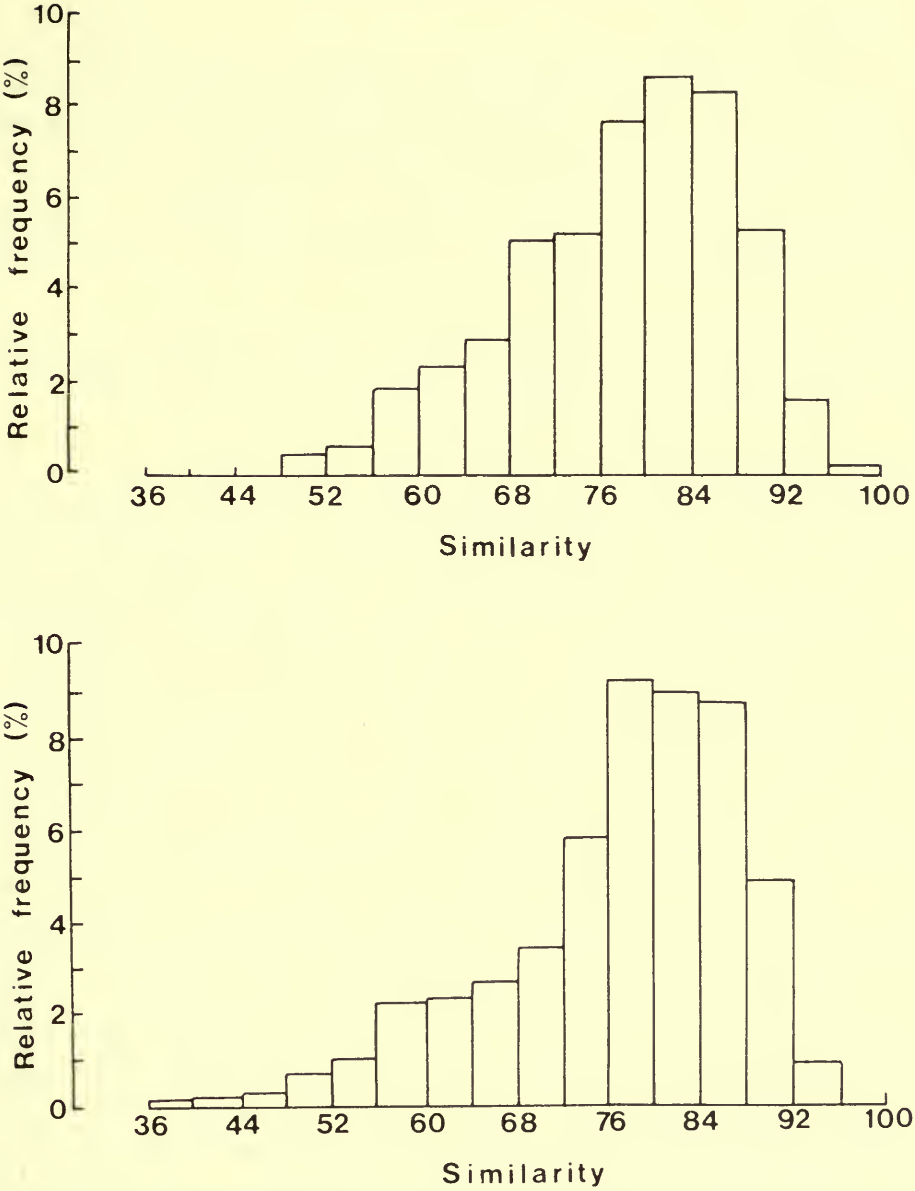


FIG. 1. Relative frequency distribution of the similarity values: a. (above) all characters; b. (below) skull and teeth only.

values observed. Such distributions are useful for assessing which values of similarity correspond to 'high' and 'low'. The distribution based on the cranial and dental characters is similar to that based on the full list but has a longer left tail with some similarity values as low as 36.

Near neighbours

A set of 666 similarities is far too large to scan by eye. Some method of arranging them is necessary and the simplest possible method is to list, for each species, the near neighbours of that species. The nearest neighbour to a species A is the species with highest similarity to A and the near-neighbour list which was used consisted of the five closest species to each species in turn, in order of similarity. Thus the set of 666 similarities is replaced by a subset of $37 \times 5 = 185$ similarities and the subset is far more readily scanned than the full set. This is due both to the reduction in the number of similarities and to the ordering in terms of similarity with each species separately.

These near-neighbour lists are extremely useful when considering the taxonomic status of each individual species and for this reason they have been included in the systematic account of each species rather than given as a separate table.

Two-dimensional plots

A good overall view of the similarities is obtained from a plot in which the points represent species and the distances between points represent taxonomic distance. This distance must be defined in terms of similarity and a mathematically convenient definition is to set the squared taxonomic distance equal to 2 (100 − similarity) so that taxonomic distance itself is the square root of this quantity. It follows that a similarity of 100 corresponds to zero taxonomic distance and a similarity of 0 corresponds to a distance of $\sqrt{200}$. The total set of such taxonomic distances may not be exactly reproducible in a plane, for three points must obey the law that the distance round two sides of a triangle is greater than the distance along the third side. If they do not, a plot is found in which the geometric distances are as close as possible to the taxonomic distances. Major groupings are usually faithfully reproduced but some taxonomic distances can be rather distorted. In this study all conclusions from plots were checked against the original list of similarities.

Fig. 2a, b shows two-dimensional plots which were prepared using the principal co-ordinates algorithm (Gower, 1966). These figures demonstrate the remote position of some of the monospecific genera (*Speothos*, *Lycaon*, *Cuon*, *Otocyon*). Within the main group the species of *Canis* are well separated from those of *Vulpes* with *Dusicyon* occupying an intermediate position. Fig. 2b, based on skull and teeth, suggests a close relationship between *Lycaon*, *Cuon* and *Speothos* (currently forming the subfamily Simocyoninae) but when all characters are considered (Fig. 2a) *Cuon* is less closely associated with this group. The close association of *Speothos* and *Lycaon* in this figure is however spurious and provides a good example of the kind of distortion that can arise in this kind of plot. The taxonomic distance between them is $\sqrt{(2 \times 32)} = 8{\cdot}0$ whereas the distance on the plot is only 0·8. On the other hand, the taxonomic distance between *Speothos* and *Vulpes bengalensis* is $\sqrt{(2 \times 41)} = 9{\cdot}0$ and the distance on the plot is 7·5. The relationship between *Speothos* (and *Lycaon*) and the Caninae is generally well represented but not the relationship between *Speothos* and *Lycaon*. The distortion could be slightly reduced by adding a third dimension, but the improvement is bought at the cost of a far more cumbersome diagram (the so-called 'plumber's diagram').

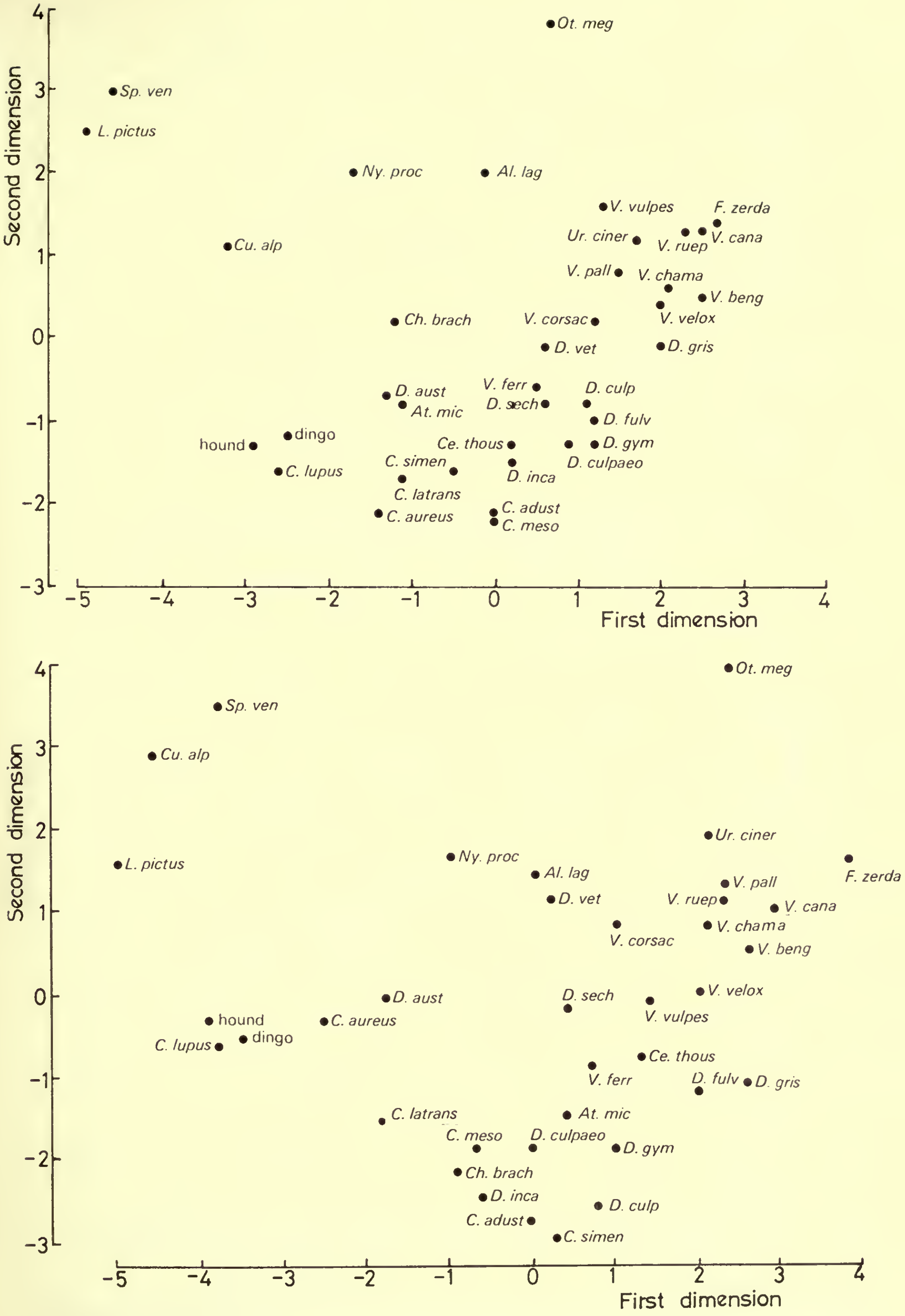


FIG. 2. Two-dimensional plot of all 37 species using the principal co-ordinates algorithm: a. (above) all characters; b. (below) skull and teeth only.

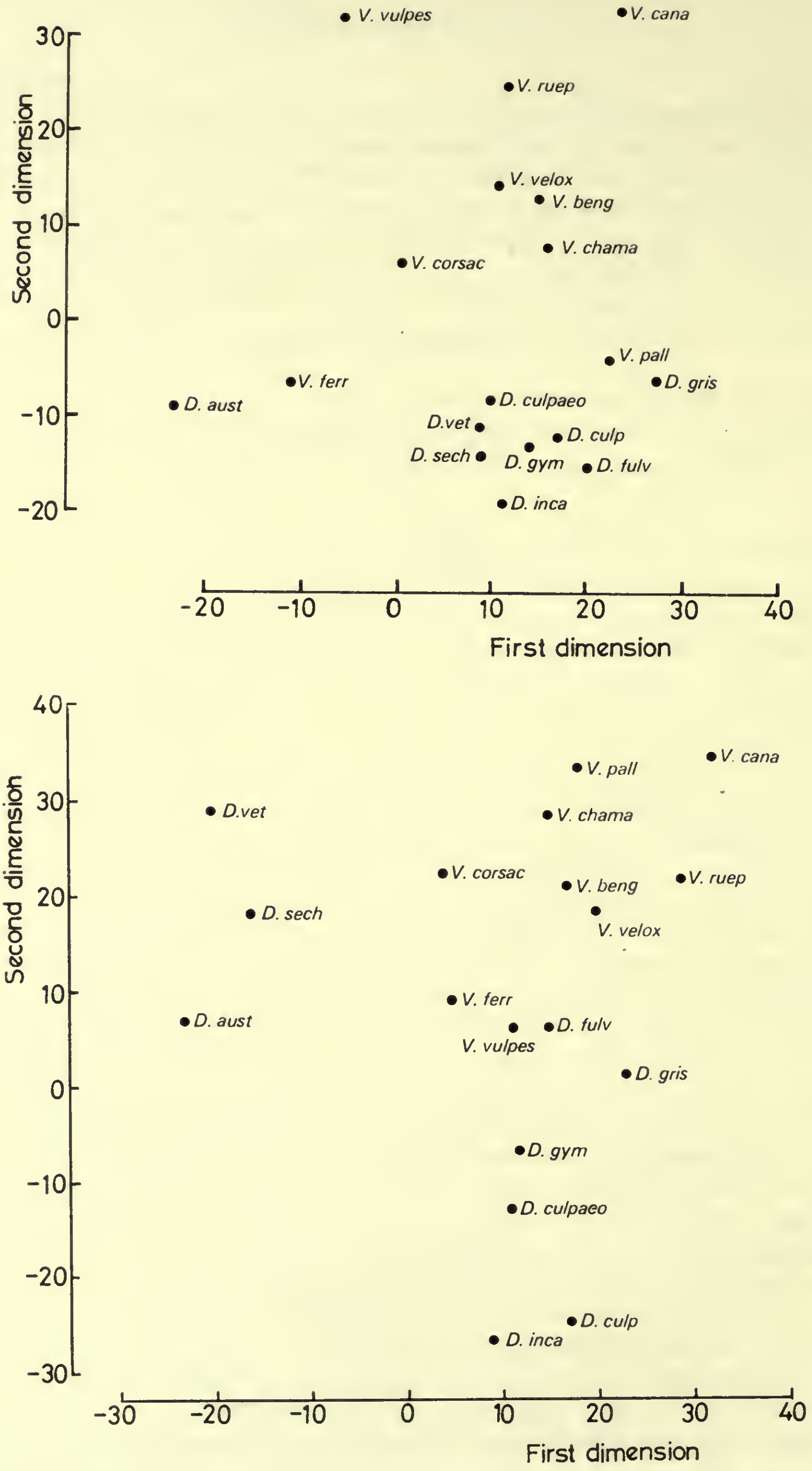


Fig. 3. Two-dimensional plot of members of *Vulpes* and *Dusicyon* using the principal co-ordinates algorithm : a. (above) all characters ; b. (below) skull and teeth only.

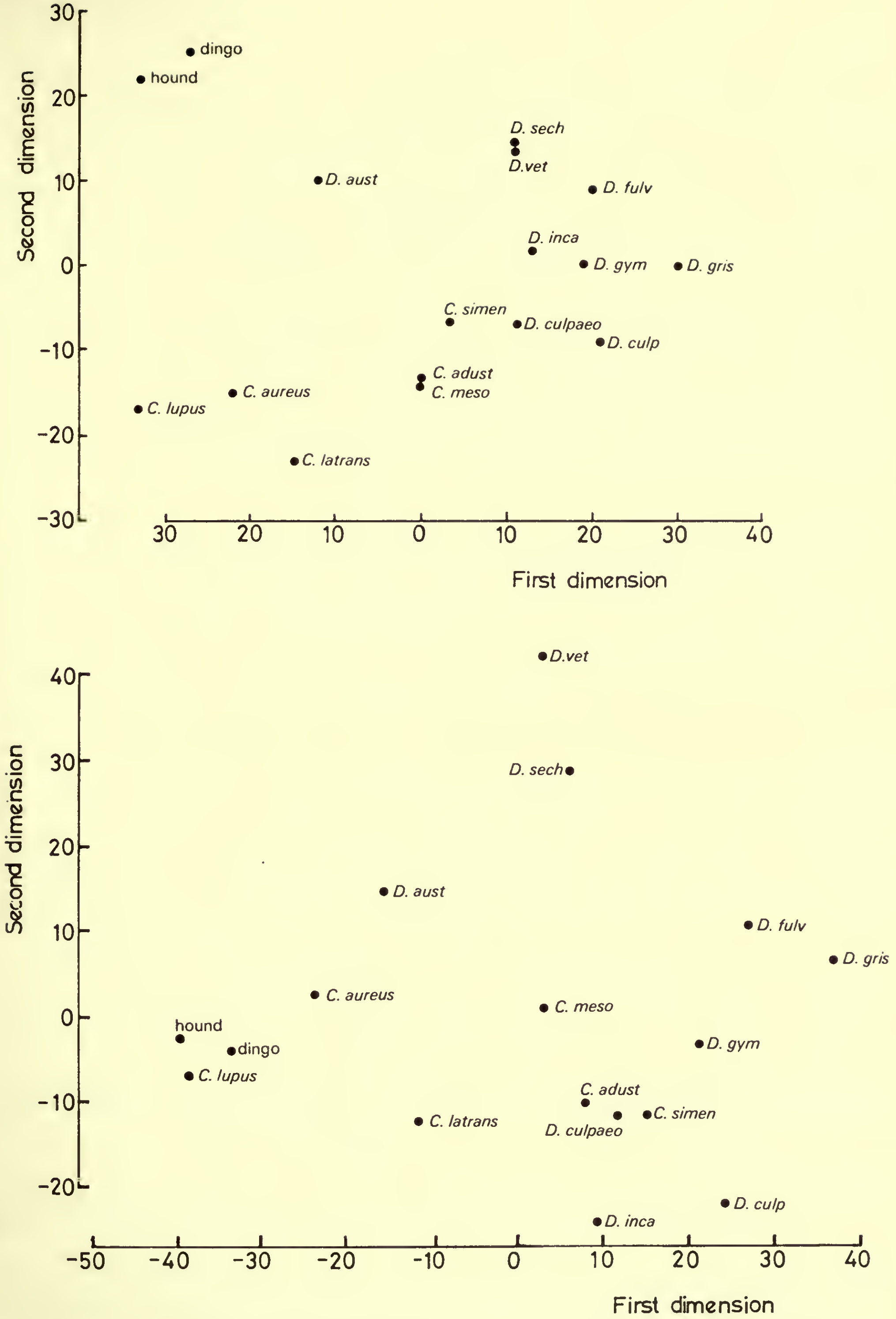


FIG. 4. Two-dimensional plot of members of *Canis* and *Dusicyon* using the principal co-ordinates algorithm: a. (above) all characters; b. (below) skull and teeth only.

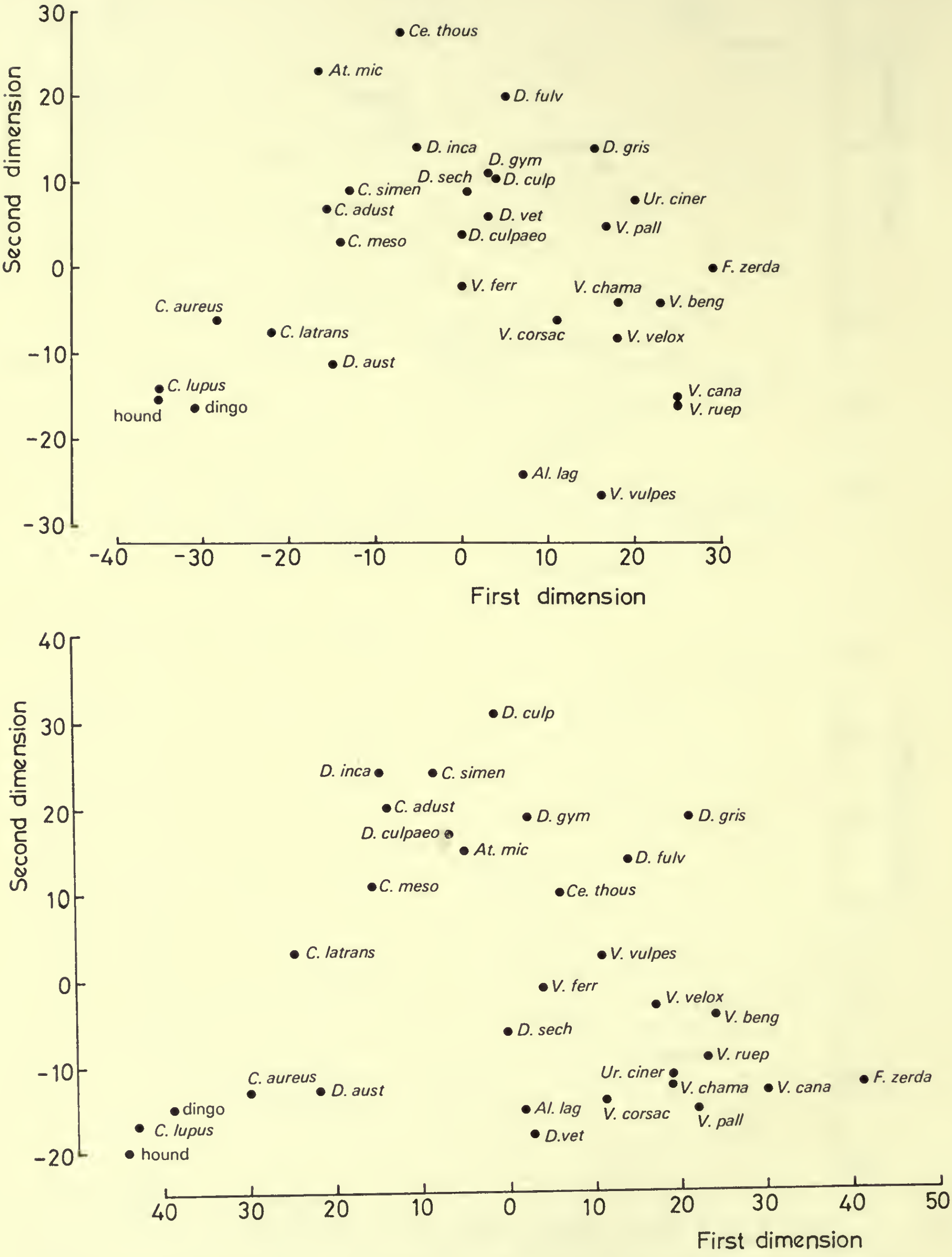


FIG. 5. Two-dimensional plot of members of the subfamily Caninae using the principal co-ordinates algorithm: a. (above) all characters; b. (below) skull and teeth only.

A better approach is to concentrate on different parts of the main plot and prepare separate plots for these parts. In this study we were interested in looking more closely at the overlap between the genera *Vulpes* and *Dusicyon* (Fig. 3a, b) and between *Canis* and *Dusicyon* (Fig. 4a, b). In Fig. 3a, using all characters, there is not much overlap between *Vulpes* and *Dusicyon* ; *V. pallida* is the most *Dusicyon*-like of the *Vulpes* (confirmed by its nearest neighbours according to similarity) and *V. vulpes* and *V. ferrilata* are rather atypical foxes ; the position of *D. australis* suggests a low similarity with both *Vulpes* and *Dusicyon*. For cranial and dental characters only (Fig. 3b) the picture does not change much although *D. sechurae* and *D. vetulus* move up closer to *D. australis* and *V. vulpes* appears more fox-like. In Fig. 4 the distinction between the genera *Canis* and *Dusicyon* is less clear than between *Vulpes* and *Dusicyon* ; the position of *D. australis* suggests a higher similarity with members of *Canis* than with *Dusicyon*, and *C. simensis*, *C. adustus* and *C. mesolomas* are all closer to the *Dusicyon* group than to other members of *Canis*. The same situation occurs in a more acute form using cranial and dental characters only.

The other aspect of Fig. 2 that is worth studying more carefully is the position of the less distinctive monotypic genera in relation to the large genera. These are shown in Fig. 5a, b. Using all characters there is a strong case for including *Urocyon* and *Fennecus* in *Vulpes*, and *Atelocynus* and *Cerdocyon* in *Dusicyon*. An additional point of interest from this figure (and Fig. 4b) is the grouping of the bloodhound, the dingo and *C. lupus*, with *D. australis* not far away. These points will be discussed in more detail in the systematic section of the paper.

Similarity values for the existing classification

The existing classification is displayed graphically in Fig. 6. The ranks of the taxa are species, genus, subfamily and family. A species such as *Otocyon megalotis* simply changes its rank as it becomes a monotypic genus and then a monotypic subfamily. If a numerical value is associated with each rank the figure becomes a dendrogram and a useful way of studying the existing classification is to construct the dendrogram based on mean similarity between species. The ranks are given numerical values as follows (similarities based on all characters).

Family – mean similarity between pairs of species, each member of the pair being from a different subfamily. There are $33 \times 3 + 33 \times 1 + 3 \times 1 = 135$ such combinations and the mean of the 135 similarities is 65·0.

Subfamily – mean similarity between pairs of species, each member of the pair being from a different genus, but the same subfamily. The number of such combinations is 431 and the mean similarity is 79·8.

Genus – mean similarity between pairs of species, each member of the pair being from a different species but the same genus. The number of such combinations is 100 (monotypic genera contribute no pairs) and the mean similarity is 87·3.

Species – this is given the value 100 which would be consistent with the way values have been given to genus if the specimens within a species were identical. In fact they were not, so the correct level for species should be rather less than 100.

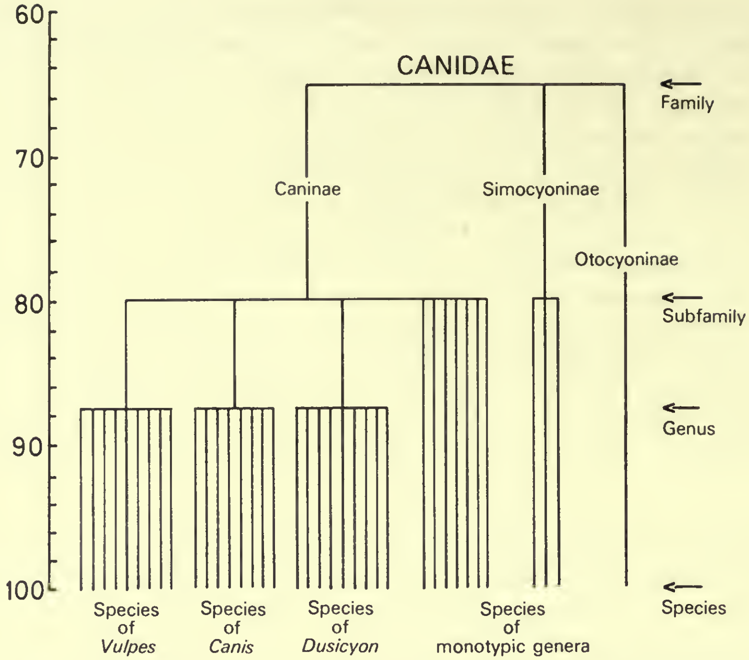


FIG. 6. Dendrogram of the existing classification : rank level equal to mean similarity between species.

To see how well this dendrogram fits the data it is necessary to examine the distribution of similarity values that go to make up each of the means described above. These are shown in Fig. 7 in the form of cumulative frequency rather than frequency distribution because the former are easier to compare. Ideally there should be little or no overlap between the ranges of values at different ranks ; such a situation would indicate a very strong hierarchic structure in the similarities. In this case the overlap is rather large, particularly between subfamily and genus, which is to say that there are too many high similarities between species from different genera within the same subfamily. It is clear from Figs 3 and 4 that there is not much one can do about this. Even if *D. australis* were to be placed in *Canis* and if *C. simensis*, *C. mesomelas* and *C. adustus* were to be placed in *Dusicyon* the hierarchic structure would still be rather weak. The overlap between the range of similarity at family and subfamily level is not so high because of the low similarity of *Otocyon megalotis* and the three members of the Simocyoninae with all other canids.

To enable impressions from the two-dimensional plots to be checked against actual similarity values a table of mean similarities between and within genera was prepared (Table 1). The mean similarities of *Fennecus* and *Urocyon* with members of *Vulpes* are in bold print, as are those of *Atelocynus* and *Cerdocyon* with members of *Dusicyon*. Apart from some distortion in Fig. 2 the plots are in good agreement with the table of mean similarities.

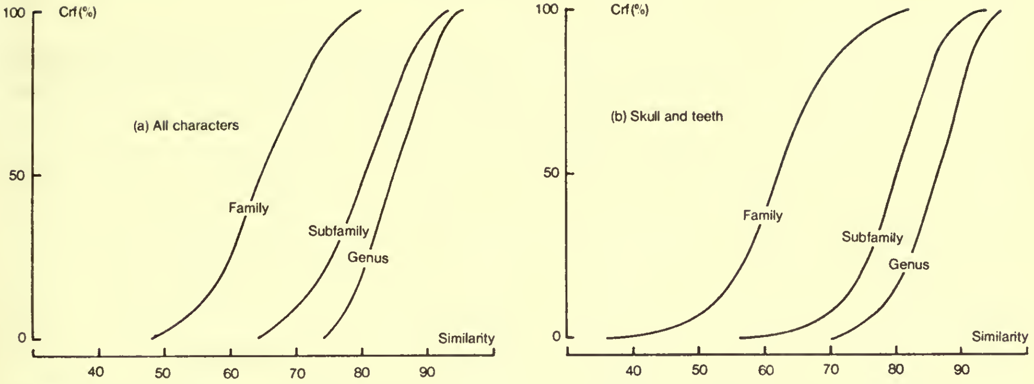


FIG. 7. Cumulative relative frequencies (Crf) of similarity values corresponding to each rank for the existing classification : a. all characters ; b. skull and teeth only.

TABLE 1

Mean similarities between and within genera of the existing classification

(a) All characters

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Vulpes	1	86·9													
Canis	2	78·0	83·9												
Dusicyon	3	86·0	83·4	90·5											
Alopex	4	79·2	74·2	79·0	*										
Fennecus	5	**85·1**	72·0	83·6	78·2	*									
Urocyon	6	**85·0**	74·8	84·5	74·4	82·5	*								
Nyctereutes	7	70·6	70·9	73·3	72·2	68·4	73·3	*							
Atelocynus	8	75·7	79·3	**82·2**	69·6	72·4	79·3	78·1	*						
Cerdocyon	9	78·0	79·4	**84·8**	72·9	76·2	82·1	76·8	86·1	*					
Chrysocyon	10	67·1	69·4	71·4	68·9	59·7	64·9	67·3	73·4	68·6	*				
Speothos	11	58·6	61·9	63·3	61·1	53·1	61·5	65·9	68·2	60·0	53·8	*			
Cuon	12	70·0	75·5	75·6	74·7	69·3	71·0	71·9	70·4	69·9	65·3	73·5	*		
Lycaon	13	57·6	62·9	61·4	61·1	51·9	55·6	57·1	56·6	53·2	50·0	67·9	69·7	*	
Otocyon	14	70·7	63·2	68·3	69·8	71·6	72·6	70·8	67·0	64·1	62·6	51·5	59·5	48·8	*

(b) Skull and teeth only

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Vulpes	1	87·6													
Canis	2	76·6	85·9												
Dusicyon	3	82·9	81·5	84·7											
Alopex	4	84·1	79·2	80·8	*										
Fennecus	5	**83·0**	64·3	74·9	77·0	*									
Urocyon	6	**81·4**	70·8	76·2	80·1	77·2	*								
Nyctereutes	7	78·0	80·0	78·7	82·9	68·4	82·2	*							
Atelocynus	8	81·5	82·2	**85·6**	78·9	71·3	81·0	82·0	*						
Cerdocyon	9	79·6	77·8	**82·6**	76·0	75·3	79·2	80·5	85·6	*					
Chrysocyon	10	75·1	83·2	79·7	76·0	63·7	73·3	74·8	82·7	75·2	*				
Speothos	11	61·7	66·1	65·1	71·3	50·0	59·2	74·1	62·5	58·6	57·3	*			
Cuon	12	62·0	70·6	65·3	71·9	50·5	58·5	72·2	63·3	57·6	63·9	87·0	*		
Lycaon	13	58·3	73·2	62·8	68·5	45·5	51·5	68·1	62·9	56·5	63·3	73·7	80·9	*	
Otocyon	14	62·7	52·2	56·9	63·8	59·6	75·9	66·0	61·5	61·4	58·4	43·0	41·7	36·6	*

Homogeneity of the three main genera

To study the effects of the marginal species on the homogeneity of the three main genera the members were listed in order of 'typicality', defined as the mean similarity of a species with all other members of the same genus. This was done both for the existing classification and for a revised classification in which the marginal fox genera, *Alopex*, *Fennecus* and *Urocyon*, are included in *Vulpes*, and *Atelocynus* and *Cerdocyon* in *Dusicyon* (see Tables 2 and 3). There are several interesting features of these lists. For the existing classification, the typicalities of *V. vulpes* and *D. australis* are relatively low. There is a high degree of concordance between the lists based on all characters and those based on cranial and dental characters only. For the revised classification the new arrivals mingle with the others in a gradual way, i.e. there is no sudden drop in typicality, except for the low typicality of *Alopex*, suggesting that it is best left out of *Vulpes*. The homogeneity is worst for the genus *Dusicyon* where similarity is based on all characters, but the new range of similarity is more in line with that for *Vulpes* and *Canis*.

TABLE 2

List of members of *Vulpes*, *Canis* and *Dusicyon* (existing classification) in order of typicality. The measure of typicality is shown next to each species

(a) All characters		(b) Skull and teeth only	
Vulpes		*Vulpes*	
V. bengalensis	90·5	*V. chama*	90·5
V. velox	89·7	*V. velox*	90·1
V. chama	89·2	*V. bengalensis*	89·9
V. corsac	88·6	*V. corsac*	88·1
V. rueppelli	88·2	*V. pallida*	88·0
V. pallida	86·0	*V. rueppelli*	87·4
V. ferrilata	84·6	*V. vulpes*	87·2
V. vulpes	83·4	*V. cana*	84·8
V. cana	82·4	*V. ferrilata*	82·6
Canis		*Canis*	
C. aureus	86·8	*C. latrans*	88·7
C. latrans	85·6	Dingo	87·8
C. mesomelas	84·8	*C. aureus*	87·3
C. adustus	84·2	*C. lupus*	86·0
C. lupus	83·0	*C. adustus*	85·8
Dingo	82·5	*C. mesomelas*	85·7
C. simensis	82·3	Hound	83·6
Hound	82·2	*C. simensis*	81·9
Dusicyon		*Dusicyon*	
D. gymnocercus	93·2	*D. gymnocercus*	88·8
D. culpaeolus	91·8	*D. culpaeolus*	87·5
D. fulvipes	91·3	*D. fulvipes*	86·4
D. griseus	91·1	*D. sechurae*	85·3
D. sechurae	90·8	*D. griseus*	85·1
D. inca	90·4	*D. inca*	83·3
D. culpaeus	90·0	*D. australis*	82·7
D. vetulus	89·3	*D. culpaeus*	82·5
D. australis	86·2	*D. vetulus*	80·4

TABLE 3

List of members of *Vulpes* plus *Alopex lagopus, Fennecus zerda* and *Urocyon cinereoargenteus;* also members of *Dusicyon* plus *Atelocynus microtis* and *Cerdocyon thous.* Both lists in order of typicality with the measure of typicality shown next to each species

(a) All characters		(b) Skull and teeth only	
Vulpes		*Vulpes*	
V. bengalensis	89·2	*V. chama*	89·1
V. chama	88·3	*V. bengalensis*	88·7
V. velox	88·3	*V. velox*	88·3
V. corsac	87·4	*V. pallida*	87·1
V. rueppelli	87·1	*V. corsac*	87·0
V. pallida	86·9	*V. rueppelli*	86·8
F. zerda	84·2	*V. vulpes*	86·2
U. cinereoargenteus	83·8	*V. cana*	83·8
V. ferrilata	83·1	*A. lagopus*	83·1
V. vulpes	82·0	*F. zerda*	81·9
V. cana	81·4	*U. cinereoargenteus*	80·9
A. lagopus	78·7	*V. ferrilata*	79·8
Dusicyon		*Dusicyon*	
D. gymnocercus	91·5	*D. gymnocercus*	88·8
D. fulvipes	90·6	*D. culpaeolus*	87·4
D. culpaeolus	90·2	*D. fulvipes*	86·7
D. griseus	89·6	*A. microtis*	85·6
D. sechurae	89·4	*D. sechurae*	85·3
D. inca	89·1	*D. griseus*	84·9
D. culpaeus	88·3	*D. inca*	83·0
D. vetulus	87·9	*C. thous*	82·9
D. australis	85·0	*D. australis*	82·7
C. thous	85·0	*D. culpaeus*	81·9
A. microtis	82·6	*D. vetulus*	80·1

Automatic classification

A natural question to ask at this stage is what happens if the 37 species are grouped using the 666 similarities with some standard linkage algorithm? The choice of linkage algorithm is never easy (see Sneath & Sokal, 1973, for a full discussion) ; several were tried and an average linkage method, equivalent to the way the dendrogram of Fig. 6 was constructed, was chosen : two groups merge at level S if the mean similarity between pairs of species, one from each group, is greater than or equal to S. A sensible name for this algorithm would be 'weighted average linkage' because the mean similarity between groups takes account of the sizes of the groups. Unfortunately 'weighted' has other connotations in taxonomy and so the term 'centroid linkage' is used instead. The reader should be warned that the terminology in Sneath & Sokal is different (1973 : 235).

The results of the algorithm are shown in Fig. 8a, b. For both 'all characters' and 'skull and teeth only' the dendrograms retain the more homogeneous parts of the main groups. At a higher level some odd combinations occur, e.g. *D. australis* with

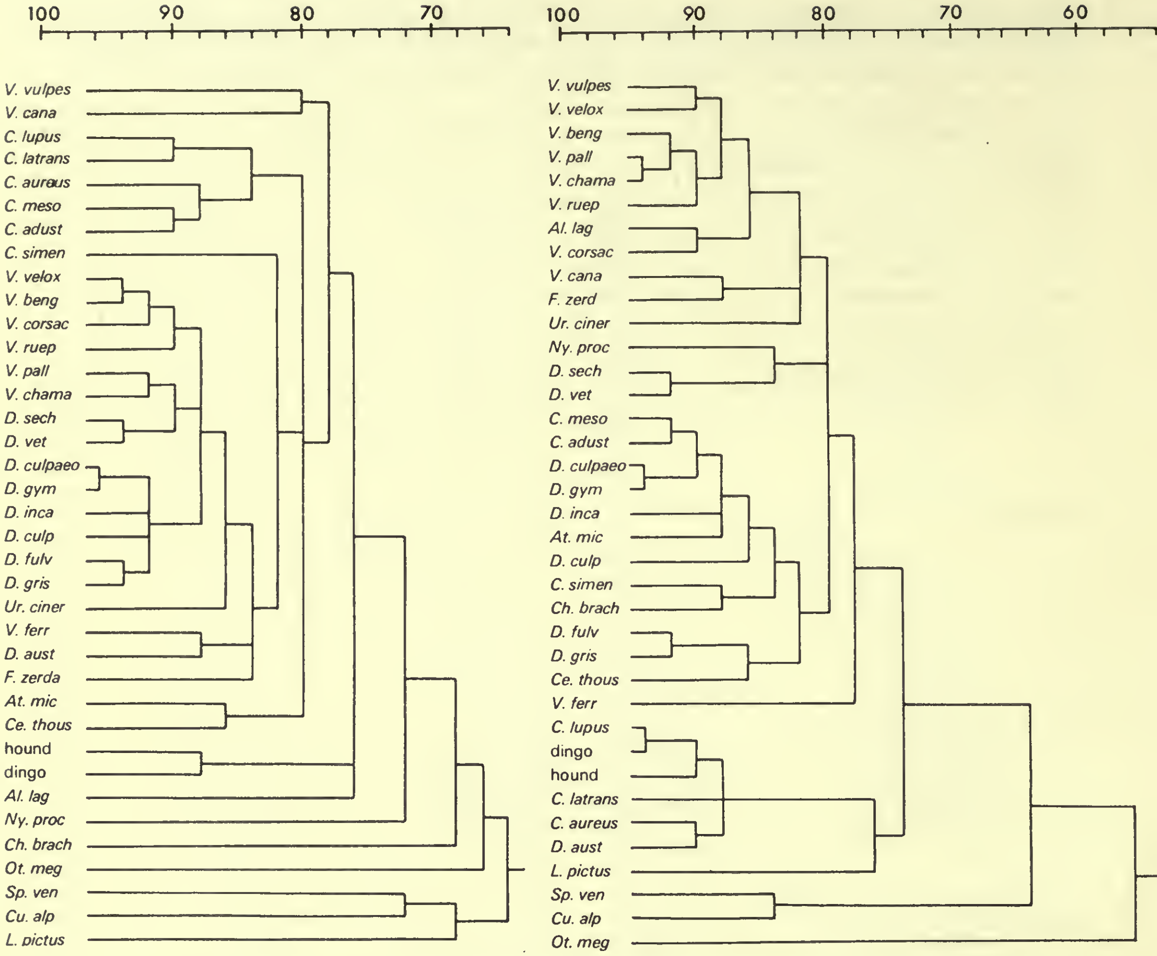


FIG. 8. Centroid linkage dendrogram : a. (left) all characters ; b. (right) skull and teeth only.

V. ferrilata which then join with the *Vulpes* and *Dusicyon* groups. Such oddities are common in average linkage dendrograms because small changes in similarity can cause large changes in the dendrogram. Another disadvantage is that the dendrogram as such gives no indication of how well a hierarchy fits the data ; further analysis along the lines followed for the existing classification would be necessary. In general, the two-dimensional plots provided a much better way of looking at the relationships between species than the dendrograms from automatic classification algorithms.

GENERAL TAXONOMIC CONCLUSIONS

Before drawing any general taxonomic conclusions from this analysis of phenetic relationships it is necessary to consider any other sources of relevant data that were not taken into account in the numerical analysis. Additional evidence might, for example, be forthcoming from the fossil record of the family, from studies of karyology, from immunology, from parasitology or from the results of attempted interbreeding, although it was believed that none of these categories of data could usefully be incorporated into the numerical analysis.

In practice the data from these additional sources proved to be so scanty that they contribute almost nothing to the problems of classification above the species level. The fossil history of the Canidae has been discussed by Matthew (1930), Romer (1955), Radinsky (1973) and Todd (1970). Data on chromosome numbers are summarized by Chiarelli (1975) who also tabulated the authorities for intergeneric hybrids. Further information on interspecific interbreeding was listed by Gray (1972). The species of lice that have been found on members of the canid family are presented in the Appendix (p. 194).

The general conclusion that emerges from the various forms of numerical analysis is that the majority of species, including most species of *Canis*, *Dusicyon* and *Vulpes*, form a large cluster with complex interrelationships and no major discontinuities, surrounded by a number of more or less distinctive and isolated species. To consider these isolated species first, the most distinctive is undoubtedly *Lycaon pictus* whose similarity to its 'nearest neighbour' is only 71. Next in order of separation come *Speothos venaticus* (73), *Otocyon megalotis* (76), *Nyctereutes procyonoides* (78), *Cuon alpinus* (79), *Chrysocyon brachyurus* (80) and *Alopex lagopus* (82). These are currently considered to represent monotypic genera except that the last (*A. lagopus*) is sometimes included in *Vulpes*. All the other species that have at one time or another been considered distinctive enough to warrant generic separation have 'nearest-neighbour' values of over 85 and are therefore no more distinctive than many species that are consistently classified within the large genera. We can therefore conclude that the species detailed above should continue to rank as monospecific genera, namely *Lycaon*, *Speothos*, *Otocyon*, *Nyctereutes*, *Cuon*, *Chrysocyon* and *Alopex*. The last of these is the least distinctive, and the skull and teeth show a very high degree of similarity to certain species of *Vulpes*, especially *V. corsac*. On the basis of all characters, however, it is clearly the most distinctive of the foxes, as shown for example by the low 'typicality' in Table 3, and there are therefore reasonable grounds for retaining it as a monospecific genus.

We can now proceed to consider whether there is justification for grouping any of these distinctive genera at subfamily level. The only such grouping with any claim to consideration seems to be the one that is currently employed, namely the grouping of *Lycaon*, *Cuon* and *Speothos* as a subfamily, contrasting with the remainder. Although many of the similarities between these are higher than between them and other species, they are nevertheless very low, ranging from 73·5 between *Cuon* and *Speothos* to 68 between *Lycaon* and *Speothos*. In contrast *Cuon* has a mean similarity of 76 with species of *Dusicyon*. In addition it must be remembered that many of the individual similarities are simply due to the shared absence of a specialized character. The higher similarity of skull and teeth between *Cuon* and *Speothos* (87) might support such a grouping but in general it seems that the similarities between these three genera (or any two of them) are so tenuous that no useful purpose is served by uniting them within a subfamily. The case for subfamily rank of any other genus is equally tenuous, e.g. *Otocyon* has an overall similarity of 73 with *Urocyon cinereoargenteus* which is normal for intergeneric similarities (Table 1).

All the remaining species that have been given generic rank emerge from this analysis as an integral part of the main cluster of species and there appear to be no grounds for continuing to place any of them in monospecific genera. These are *Fennecus* and *Urocyon* which fall clearly within *Vulpes* ; and *Cerdocyon* and *Atelocynus* which fall so close to *Dusicyon* that it seems reasonable to include them (Figs 1 and 5, Table 3). The status of all these is considered in more detail in the systematic section.

The question of the recognition of generic limits within the *Canis/Vulpes/Dusicyon* complex is more difficult. No objective analysis of the results of this study would produce these three genera as presently composed but nor would it produce any other clear-cut grouping of species. On the other hand, the retention of these genera does not produce any serious anomalies and they are capable of definition. They are therefore retained here. Arising from a detailed study of the South American species, Langguth (1975) proposes to recognize *Cerdocyon thous*, *Atelocynus microtis* and *Lycalopex vetulus* as additional, monotypic, 'differentiated' genera and to include the remaining species of *Dusicyon* in *Canis*. These proposals are not greatly at variance with our conclusions although the distinctiveness of these 'differentiated' species seems marginal, and if *Dusicyon* were merged with *Canis* it would be difficult to argue that *Vulpes* should not be treated likewise.

This examination of the family Canidae as an integrated whole has enabled some anomalies in the taxonomy to be straightened out. It is hoped that it has also enabled some misconceptions to be erased. Perhaps the most notable of these is the belief that the common fox, *Vulpes vulpes*, is a typical representative of its genus. This belief has led to the classification of those species of fox that do not conform with *V. vulpes* in separate genera. In fact the typical fox is *Vulpes bengalensis* and *V. vulpes* should be considered almost as an aberrant species. When this fact is recognized the classification of the genus becomes more straightforward.

The extinct Falkland island wolf, *Dusicyon australis*, is seen to be a very anomalous species but lack of adequate specimens precludes any very clear assessment of its affinities.

The revised classification proposed is presented below, and the relationships of each genus and species are considered in more detail in the systematic account that follows. In this list the 'species' of *Dusicyon* that are indented may be conspecific with the species listed above them, but this is a question that can only be answered by more detailed study of distribution and variation in South America.

Proposed classification of the family Canidae:

Canis lupus	Wolf
(*Canis rufus*)	(Red wolf)
Canis (domestic)	Dingo and domestic dogs
Canis latrans	Coyote
Canis aureus	Golden jackal
Canis mesomelas	Black-backed jackal
Canis adustus	Side-striped jackal
Canis simensis	Ethiopian jackal
Vulpes vulpes	Common or red fox
Vulpes corsac	Corsac fox
Vulpes ferrilata	Tibetan sand fox
Vulpes bengalensis	Bengal fox
Vulpes cana	Blanford's fox
Vulpes rueppelli	Sand fox
Vulpes pallida	Pale fox
Vulpes zerda	Fennec fox
Vulpes chama	Cape fox
Vulpes velox	Kit fox
Vulpes cinereoargenteus	Grey fox
(*Vulpes littoralis*)	(Island grey fox)
Alopex lagopus	Arctic fox
Otocyon megalotis	Bat-eared fox
Nyctereutes procyonoides	Raccoon dog
Dusicyon australis	Falkland Island wolf – extinct since *c.* 1880
Dusicyon culpaeus	Colpeo fox
Dusicyon culpaeolus	
Dusicyon gymnocercus	Azara's fox
Dusicyon inca	
Dusicyon griseus	Argentine grey fox
Dusicyon fulvipes	Chiloe fox
Dusicyon sechurae	Sechura desert fox
Dusicyon vetulus	Hoary fox
Dusicyon thous	Common zorro
Dusicyon microtis	Small-eared zorro
Chrysocyon brachyurus	Maned wolf
Speothos venaticus	Bush dog
Cuon alpinus	Dhole
Lycaon pictus	Hunting dog

SYSTEMATIC ACCOUNT

Genus *CANIS* L.

Type species *Canis familiaris* L., the domestic dog.

For the purposes of this analysis the genus has been taken as comprising six species plus two domesticated forms, the feral dingo as an example of a primitive domestic breed and the bloodhound which exemplifies advanced domestication without gross abnormalities. These two dogs have been treated as separate 'species' on an equal level with the wild species. Although *Canis familiaris* is the type species for the genus the name has not been used in this work because we believe that formal zoological nomenclature should be avoided in naming domestic animals (see Groves, 1971).

Recent classifications of the Canidae usually include the three groups, wolves, coyote and jackals, within the genus *Canis* and the results of this numerical taxonomy show that this is consistent with the phenetic relationships of the species. Heller (1914) separated the jackals from the wolves and coyote in the genus *Thos* Oken, and this classification was followed by Allen (1939). Heller defined the genus *Thos* as a group of Canidae having long slender *Vulpes*-like canines, small outer incisors, small carnassials, upper molar teeth with well-marked cingula and the fourth lower premolar with a minute extra cusp on its hinder border. He distinguished the genus *Canis* by the much thicker and shorter canines, greatly enlarged outer incisors, large carnassials, molars without a definite cingulum, and the fourth lower premolar without a third cusp on its posterior border. None of these characters is definitive and they are all very variable in their development. It is therefore more appropriate to include the jackals within the genus *Canis*. Allen (1939) also afforded separate generic status to the Ethiopian jackal, *Canis simensis*, placing it in the genus *Simenia* Gray. This somewhat aberrant canid appears from the results of the numerical taxonomy to be phenetically close to the genus *Dusicyon* but the skull has a high similarity with that of *Canis adustus* and we therefore include it with the jackal group in the genus *Canis*. There is no evidence to support the suggestion of Brink (1973) that *C. adustus* should be placed in a separate genus.

The wolf is the largest species within the family and it is separated from the coyote and jackals by its more highly evolved social behaviour patterns that are closely reflected in its descendant, the domestic dog. The skull in all members of the genus has well-defined diagnostic features. It is always rather heavy and has large frontal sinuses. The temporal ridges are close together and are often fused into a strong interparietal crest. With the exception of *Canis simensis*, the facial region is relatively shorter than in the genera *Vulpes* or *Dusicyon*. The canine teeth are robust and the carnassials are relatively large. There is no subangular lobe to the mandible.

The genus is very flexible in its habitat preferences, again with the exception of *C. simensis* which is confined to montane areas of Ethiopia, where it is nearly extinct. Most wild *Canis* species have wide distributions but they are not found in areas of dense tropical rain forest. The domestic dog has been taken to all parts of the world that are inhabited by man and it is presumed that the dingo was taken to Australia by man during prehistoric times. The wild members of the genus *Canis* are distributed throughout Europe, Asia, North America and Africa.

Canis lupus L., 1758

Wolf

Distribution. Widespread in the northern hemisphere and as a species without particular habitat preferences. May be found in tundra regions, woodland, open plains or the edges of desert areas, from sea level to more than 3000 m. As their habitat has been restricted the wolf populations have been moved into progressively more inhospitable regions. Formerly widespread throughout the temperate areas of the northern hemisphere, but now extinct in western Europe except for small dwindling populations in Portugal, Spain, Italy, Sicily and Scandinavia. Still widely distributed in the U.S.S.R. and extending eastward into Mongolia, western China, Korea, Tibet and southwards into India. There are still small numbers in southwestern Asia. Widespread in Canada and Alaska but extinct in the U.S.A. except in wildlife parks. Classified as a vulnerable species by the *Red data book* (Goodwin & Holloway, 1972).

DESCRIPTION. The largest member of the family. Body heavy with large head and long legs. Tail long and bushy. Ears erect. Fur very thick and with long guard hairs, especially in the arctic regions of the range. Pelage characters very variable – may be white, tawny, grey or black, but grey agouti with some tawny is the predominant colouring. Legs, ears, muzzle and underparts are usually reddish or pale. There is often a dark saddle and a dark patch over the tail gland. Highly social. Hunt large prey in packs of between two and eight individuals, although larger groups may be found in exceptional circumstances (Mech, 1970).

Skull large with very well-developed interparietal crest. Massive jaws with powerful canine and carnassial teeth. Facial region long. Bullae large.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Canis latrans	90·0	Dingo	94·7
Canis aureus	87·7	Bloodhound	92·4
Bloodhound	84·0	*Canis aureus*	89·2
Dusicyon culpaeolus	82·0	*Canis latrans*	89·1
Canis mesomelas	81·8	*Dusicyon australis*	87·5

It is of great interest that the numerical results show such a close phenetic similarity between *Canis lupus*, the dingo and the bloodhound, especially as this breed of dog bears little superficial resemblance to the wolf. This is discussed in the following sections on the dogs. The wolf is also closely related to the coyote, *Canis latrans*, and it may be mentioned here that there is evidence to suggest that *Canis rufus* Audubon & Bachman, 1851 (formerly known as *Canis niger* Bartram, 1791 – see Paradiso & Nowak, 1972), which has not been included in this analysis, is a composite species resulting from wolf–coyote hybrids (see Lawrence & Bossert, 1967, 1975 ; Mech, 1970 ; Paradiso, 1971 ; Gipson *et al.*, 1974).

REMARKS. *Canis lupus* (when not persecuted by man) is one of the most widespread and successful of large mammals. It is exceedingly variable in size, pelage and body proportions, but probably not in its behaviour patterns, over its wide range. For the purposes of this analysis four specimens were chosen for measurement and scoring of characters, the localities being selected to cover as much as possible of the range. The localities were Sweden, British Columbia, Spain and India. Indian wolves are considerably smaller than northern animals and have a shorter coat.

In order that a predator may kill its prey efficiently it must be either larger than or approximately the same size as the prey or it must hunt in a group and use a concerted effort to obtain its food. The wolf is adapted to feed on animals that are much larger than itself and the features that distinguish it from other canids are all integrated with this predator–prey relationship which has resulted in a highly evolved social system. The wolf pack is held together by strong social bonds and the suppression of aggression between individual members.

So much work has been carried out in recent years on the social behaviour and signals of communication in the wolf and it is now so well known that it will not be repeated here (amongst others, see Crisler, 1959; Fox, 1970, 1971, 1975; Mech, 1970; Pulliainen, 1967; Schenkel, 1967; Scott, 1967; Woolpy & Ginsburg, 1967). It may be said, however, that the basic difference between the wolf and the other highly social canid, *Lycaon pictus*, is that the wolf pack is based on a hierarchical system (as in man) whereas in *L. pictus* the pack is held together by individual dominant and submissive relationships, with no established hierarchy and no highly evolved system of communication by facial and body signals (Fox, 1970; see p. 181).

Canis (domestic)

Dingo

Distribution. Open country throughout most of the continent of Australia except Tasmania. Absent from central New South Wales and the northern agricultural districts of western Australia (Ride, 1970).

Description. A medium to large-sized dog. Usually a tawny-yellow colour but may show other colour variations including black. There is often a white tip to the tail and white feet. Of 15 skins examined in the British Museum only one had the first digit on the hind feet represented by a claw ('dew claw'). As noted by Lönnberg (1916), a vestigial first digit may be very occasionally present in wild canids but it is certainly exceptional. Mivart (1890, p. iv) stated that no wild species of canid ever has this first digit and we have not noticed any example of it, but it is relatively common in domestic dogs. The same dingo skin that had 'dew claws' (no. 25.8.1.9) had a slight dark patch on the dorsal side of the tail in the position of the tail gland. Hildebrand (1952b) quoted the belief that the tail gland is not found in the domestic dog, but further observation might well show that it can be present.

Skull like that of a small wolf. Teeth large and evenly spaced, carnassials strongly developed. Bullae large but rather flatter than in the wolf. Frontal sinuses well developed.

Systematic position. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Bloodhound	88·7	*Canis lupus*	94·7
Dusicyon australis	87·1	*Canis latrans*	91·7
Canis aureus	84·0	*Canis aureus*	91·5
Dusicyon inca	83·5	*Dusicyon australis*	91·1
Dusicyon sechurae	83·3	Bloodhound	90·9

The dingo is a fascinating relic of the primitive domestic dogs that must have been widespread in Asia during the early Holocene. It is not a biological species but a feral dog that is closely related to the New Guinea singing dogs and Indian pariah dogs. It is probable that these dogs are all directly descended from the Indian wolf, *Canis lupus pallipes* Sykes, 1831. This supposition is supported by the 'near neighbours' table for skull characters which shows a similarity of nearly 95 for the dingo and the wolf. The only other taxa in this analysis that are linked at this high level of similarity are *Dusicyon gymnocercus* with *Dusicyon culpaeolus* (which may well not be separate species) and *Vulpes chama* with *Vulpes pallida*. Corbett & Newsome (1975) have made a preliminary analysis of the social behaviour of the dingo in the wild.

On the two-dimensional plots the dingo, wolf and bloodhound can be seen to be closely linked, and on the 'near neighbours' table for cranial and dental characters the dingo is linked with the 'typical' species, *Canis aureus* and *Canis latrans*, at a similarity of just under 92.

The enigmatic position of *Dusicyon australis*, the extinct Falkland Island wolf, in association with the dingo and bloodhound is discussed in the section on that species (p. 166).

Canis (domestic)

Bloodhound

Origin. The bloodhound is probably descended from the French black and tan hounds that were bred for several hundred years at the St Hubert Monastery in the Ardennes. It has been established as a British breed since the Medieval period.

Description. A pure-bred hound of ancient descent. Large, massively built, short-coated with long pendulous ears, a wrinkled face and long tail. May be black and tan, all tan or red and tan ; the skin that was used for this project was a mottled grey and tawny. The first digit on the hind foot (hallux) is sometimes developed as a 'dew claw' as is common in all domestic dogs. No black patch on the dorsal part of the tail in the position of the tail gland. Like all domestic dogs the bloodhound is a highly social animal.

Skull typically 'hound-like'. Facial region long with heavy jaws. Teeth large and well-spaced but carnassial teeth relatively short. Postorbital processes of the frontal bones much swollen so that the profile of the skull has a marked 'stop'. This is a characteristic feature of advanced domestication in the dog and is associated with enlarged frontal sinuses. The reduced carnassial teeth and rather small flat bullae are also features of domestication. The interparietal crest is usually well-developed.

Systematic position. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Dingo	88·7	*Canis lupus*	92·4
Dusicyon australis	85·9	Dingo	90·9
Canis lupus	84·0	*Canis aureus*	86·3
Canis aureus	83·5	*Canis latrans*	85·4
Canis latrans	81·1	*Dusicyon australis*	85·3

It has been known for some years, from studies of social and agonistic behaviour, that the domestic dog is more likely to be descended from the wolf than from the coyote or the jackal (see, for example, Scott, 1967). It is most interesting that our numerical results, which included only a few behavioural characters out of the total of 90, so closely corroborate this deduction. Previous work on the osteological differences between the skulls of dogs and the wild *Canis* species has often failed to show clear distinction between the different groups. The present analysis shows that the skull of the bloodhound is phenetically closer to that of the wolf and the dingo than it is to the skulls of coyote or jackal. The two-dimensional plots and centroid linkage dendrogram also show the same relationships.

It is surely rather remarkable that the dingo and the bloodhound, which bear so little superficial resemblance to each other and have such widely separated origins, should be so phenetically similar. The inference must be that they share a common ancestor in the wolf.

Canis latrans Say, 1823

Coyote

Distribution. Widespread in North America. Formerly confined to areas west of the Mississippi river from southern Canada to central Mexico ; now extending to Alaska and Costa Rica but still not very common in the eastern regions. The preferred habitat is open plains and desert and the coyote is not found in damp tropical areas (Hershkovitz, 1972 : 359 ; Miller & Kellogg, 1955 ; Van Wormer, 1964).

Description. 'Wolf-like' but smaller. An adult North American male wolf weighs an average of 45 kg, whereas the average weight of a male coyote is only 12 kg (Mech, 1970 ; Van Wormer, 1964). The coyote stands nearly as high at the shoulder as the wolf but it is much more lightly built with long slender legs, large ears and a bushy tail. Pelage characters are variable as with all canids that cover a wide geographical range. The coat is usually long and has an overall buffy-grey colour with long dark-banded guard hairs. Legs and sides may be fulvous. Underparts and chin pale or nearly white. Tip of tail usually black. Not highly social but may live in family groups and take part in communal howling. Feeds on rodents, small game animals and birds.

Size of skull between that of a small wolf and a jackal. The teeth, especially the canines and carnassials, well developed. Interparietal crest present but not so pronounced as in the wolf. Bullae rounded. Differences between the skulls of wolves, coyotes and domestic dogs have been analysed by Lawrence & Bossert (1967).

Systematic position. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Canis lupus	90·0	Dingo	91·7
Canis aureus	89·7	*Canis mesomelas*	90·8
Dusicyon culpaeolus	87·5	*Canis lupus*	89·1
Canis mesomelas	87·4	*Canis aureus*	88·9
Dusicyon culpaeus	87·2	*Dusicyon australis*	88·9

On phenetic characters the coyote lies between the wolf and the jackals. It is unlikely that the coyote has played any great part in the origins of the domestic dog. The American Indians may have crossed their dogs with coyotes from time to time but it is probable that this had only a local effect. Mengel (1971) has shown that gene flow from dogs to wild populations of *Canis latrans* (and also to *Canis lupus*) is unlikely to occur because of a phase shift in the breeding time of the hybrids. This prevents further reproduction after the first generation. An interesting aspect of Mengel's work was his demonstration that wild male coyotes are only fertile for about two months in the year whereas male domestic dogs are always in breeding condition.

Canis aureus L., 1758

Golden jackal, Asiatic jackal

DISTRIBUTION. Wooded and open country in the Balkan states, Romania, countries of the eastern Mediterranean, including Greece, Libya, Egypt and westwards into Morocco. South to Senegal, the Sudan, Somalia, Ethiopia and Kenya. Eastwards through western Asia, the Middle East, Baluchistan and Sind. Throughout the peninsula of India to Ceylon and east to Assam, Burma and Thailand (Ellerman & Morrison-Scott, 1966).

DESCRIPTION. Like the coyote, this jackal covers a very wide geographical area and it is very variable in size and pelage characters. The skins in the British Museum from localities in S.W. Asia and S.E. Europe were described in detail by Pocock (1938). In general the fur is rather coarse and not very long. The dorsal area is mottled black and grey. The head, ears, sides and limbs may be tawny or rufous, the underparts pale ginger or nearly white. Tail tip black. Feeds on small animals, carrion, insects and some fruit and vegetable matter. Not highly social but will hunt in packs. An exceptionally large subspecies, *C.a. lupaster* Hemprich & Ehrenberg, 1833, occurs in Egypt and Libya ; a specimen of this subspecies was included in the analysis.

Skull like that of a very small wolf, with well-developed, high-crowned teeth. Interparietal crest present. Facial region somewhat short. There is often a well-marked cingulum on the labial side of M^1.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Canis mesomelas	89·9	Dingo	91·5
Canis latrans	89·7	*Dusicyon australis*	91·4
Dusicyon australis	88·8	*Canis lupus*	89·1
Canis adustus	88·7	*Canis latrans*	88·9
Canis lupus	87·7	*Canis mesomelas*	88·3

For the all-characters similarity *Canis aureus* is the most typical of the *Canis* species (Table 2) and this is in fact obvious from one look at this jackal, for it is of medium size and has no outstanding features. The pelage is typical of the family and the wide range that it covers precludes specialization. The skull of *C. aureus* is not as similar to the African jackals, *Canis mesomelas*, *Canis adustus* and *Canis simensis*, as it is to the dingo, wolf or coyote which is somewhat surprising. The position and relationships of *Dusicyon australis* are anomalous and are discussed in the section on that species. The behaviour of the golden jackals of the Ngorongoro Crater in Tanzania has been studied by H. & J. van Lawick-Goodall (1970), and detailed observations were made on a pair of jackals in Israel by Golani & Keller (1975).

Canis mesomelas Schreber, 1778

Black-backed jackal

DISTRIBUTION. Widespread in open savannah throughout eastern and southern Africa, northwards to the Sudan and west to Cameroun (Allen, 1939; Ellerman *et al.*, 1953).

DESCRIPTION. Distinguished by the dark saddle which extends the length of the back to the black tip of the tail. This saddle, which is mottled black and cream, contrasts strongly with the rufous sides of the body. The head and ears are also rufous flecked with white and dark hairs. The limbs are tawny or rufous, the underparts pale ginger. Underfur, except on the abdomen, consistently rufous, the colour of the saddle being due to banded black and white guard hairs. Lives alone or in small family groups. As with all species of *Canis* this jackal may participate in communal howling. Feeds on small prey and carrion.

Skull smaller than that of *Canis aureus*. Parietal crest may be poorly developed and there may be a narrow lyriform sagittal area enclosed by weak temporal ridges. Dentition, especially the canines which are rather pointed, may resemble that in the genus *Dusicyon*.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon culpaeolus	92·9	*Canis adustus*	92·7
Dusicyon gymnocercus	91·5	*Dusicyon australis*	92·5
Canis adustus	90·3	*Dusicyon culpaeolus*	91·9
Canis aureus	89·9	*Canis latrans*	90·8
Dusicyon inca	88·7	*Dusicyon gymnocercus*	90·7

The two-dimensional plots and centroid linkage dendrograms show that *Canis mesomelas* and *Canis adustus* are closely related and they have a similarity of 92 on cranial and dental characters.

REMARKS. The black-backed jackal is looked upon as vermin in South Africa and it is persecuted by farmers because it kills sheep.

Canis adustus Sundevall, 1846

Side-striped jackal

Distribution. Covers the same regions as *Canis mesomelas*, but prefers a heavier density of vegetation and wooded areas. Widespread in southern and eastern Africa. Northwards into the Sudan and Cameroun (Ellerman *et al.*, 1953).

Description. The pelage of this jackal differs considerably from that of *C. mesomelas* and it is a larger, heavier animal. The coat is long and soft-haired. There is no marked saddle but a line of white guard hairs, followed below by a line of dark hairs, runs along each side of the body, giving the jackal its name. The underfur is ochreous, the guard hairs banded dark and white, giving a generally mottled grey appearance to the pelt. Head buffy-grey with darker grey ears. Underparts pale grey. Tail tip white. Feeds on carrion, rodents, insects and vegetable matter.

Skull slightly longer and narrower than that of *C. mesomelas*, but the teeth are smaller and less high-crowned, especially the carnassials. The bullae are smaller and flatter. Interparietal crest slightly developed.

Systematic position. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Canis mesomelas	89·9	*Canis mesomelas*	92·7
Canis latrans	89·7	*Dusicyon culpaeolus*	92·0
Dusicyon australis	88·8	*Dusicyon gymnocercus*	91·5
Canis aureus	88·7	*Canis simensis*	91·2
Dusicyon inca	88·5	*Dusicyon microtis*	90·4

As stated above, it is clear from the numerical results that *Canis adustus* has a high similarity with *C. mesomelas*. According to Van der Merwe (1953) this jackal is mainly nocturnal and feeds on smaller prey than the black-backed jackal. Certainly the relative conformation of its skull and teeth suggest that this is likely. The side-striped jackal has no reputation as a killer of sheep and consequently it is not exterminated by farmers in the same way as *C. mesomelas*. These two jackals are a good example of closely related sympatric species.

Canis simensis Rüppell, 1835

Ethiopian jackal, Simien jackal

Distribution. Montane; inhabits grassland plateau areas associated with giant lobelia at an altitude of 2900 to 3900 m on the Simien and other mountains in central Ethiopia. Probably nearly extinct and classified as an endangered species in the *Red data book* (Goodwin & Holloway, 1972).

Description. Very little is known about this rare canid. The overall colour is a tawny rufous with pale ginger underfur. The chin, insides of ears, chest and underparts are white. There is a distinctive white band around the ventral part of the neck and the inner sides of the limbs are also white. The tail is rather short; the posterior end is dark with black ends to the guard hairs; the anterior part is white underneath and around the anus. There is no dark patch to mark the tail gland.

Skull 'jackal-like' but with an elongated facial region. Teeth, especially the upper carnassials, rather small. Canines long and sharply pointed. Interparietal crest slightly developed.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon gymnocercus	88·5	*Canis adustus*	91·2
Dusicyon inca	87·6	*Dusicyon gymnocercus*	89·7
Dusicyon culpaeolus	87·3	*Chrysocyon brachyurus*	88·7
Dusicyon fulvipes	86·1	*Dusicyon culpaeolus*	88·5
Dusicyon culpaeus	86·1	*Dusicyon culpaeus*	86·5

Canis simensis is sometimes called the Simien fox. It is not, however, at all closely linked to the *Vulpes* group and the postorbital processes of the frontal bones do not have the little depressions that signify the lack of frontal sinuses; a character that within the Canidae is only found in the genera *Vulpes*, *Alopex* and *Otocyon*.

The near-neighbours tables and two-dimensional plots show a seemingly close similarity with the genus *Dusicyon* but it can be seen that both *Canis adustus* and *Canis mesomelas* are also close to *Dusicyon*, and it is possible that the numerical results for *C. simensis* are biased by lack of data on the postcranial skeleton and on behaviour. Gray (1868) placed this species in a separate genus, *Simenia*, and this classification was followed by Allen (1939). However, the 91·2 similarity that the cranial and dental characters have with *C. adustus* shows that separate generic status is not justified and the species is therefore retained within the genus *Canis*. In general appearance the skull of *C. simensis* looks like an elongated skull of *C. adustus*, in the same way as, in the foxes, the skull of *Vulpes ferrilata* looks like an elongated skull of *Vulpes corsac*. It may be worth comment that both *C. simensis* and *V. ferrilata* are adapted to a montane environment.

Genus **Vulpes** Frisch, 1775

Type species *Canis vulpes* L. 1758.

The work of Frisch (1775) has been declared unavailable by the International Commission on Zoological Nomenclature (Anon., 1950). This author was accepted by Simpson (1945) and is used here because the next available uses of *Vulpes* (Bowdich, 1821; Fleming, 1822) postdate the generic name *Fennecus* Desmarest, 1804 (Oken, 1816 also being unavailable, see Opinion 417, 1956). As we propose in this classification to include *Fennecus zerda* with the foxes this would mean changing the generic name for the entire group of foxes from *Vulpes* Fleming, 1822 to *Fennecus*

Desmarest, 1804 if Fleming were accepted. This change would clearly be most impractical, as *Vulpes* is in such general use. A proposal has therefore been submitted to the Commission to place *Vulpes* Frisch, 1775 on the Official List of Generic Names in Zoology (Clutton-Brock & Corbet, 1975).

The genus *Vulpes* covers nearly the same geographical range as *Canis* except that there is no species of fox in central Africa. Twelve species have been included in this classification. As well as all those that are generally recognized as true foxes it has been found necessary to include the fennec fox (*Fennecus zerda*), and the American grey fox (*Urocyon cinereoargenteus*). Justification for the changes are given on p. 134 and in the sections on these species.

All the species of fox are solitary carnivores and they mostly live in burrows that they dig themselves. They prey on small mammals, birds, reptiles, insects and eggs, whilst some species feed on a considerable amount of fruit and vegetable matter. All foxes have a pointed muzzle, large erect ears and a long bushy tail. They tend to be rather low-bodied and have long, thick fur, but the wide distribution of the genus is reflected in modifications to these characters, as for example in adaptations to desert and montane conditions.

The skull of all members of the genus *Vulpes* is distinctive in that the frontal sinuses are only slightly developed, if present at all, and there are small depressions that can be seen and felt on the frontal bones just medially from the postorbital processes. It may be noted that the skulls of *Vulpes zerda*, *Vulpes cinereoargenteus* and *Alopex lagopus* show these depressions and so, incidentally, does the skull of the South African bat-eared fox, *Otocyon megalotis*. In all foxes the skull is slender and flattened compared to that of *Canis*. The temporal ridges may be nearly fused as in *Vulpes vulpes* or they may be indistinct and wide apart as in the desert foxes. The raised temporal ridges and rugose parietal bones of *V. cinereoargenteus* can be seen as an exaggerated form of a common character when the genus is looked at as a whole. The sagittal and parietal bones of *Vulpes pallida*, in fact, closely resemble those of *V. cinereoargenteus* but are, in comparison, only feebly developed.

Huxley (1880) made a comprehensive comparative study of the skulls and dentition of *V. vulpes* and *Dusicyon culpaeus* as a basis for his wider study of the whole family Canidae. He concluded that although the skulls of the two species were very alike there were outstanding differences in the absence or slight development of the frontal sinuses in the fox and in the relative shapes of the cranial cavities, reflecting the shape of the brain. On these differences Huxley divided the Canidae into two groups, the alopecoids which included all the true foxes, and the thooids which included *Canis*, *Dusicyon* and *Lycaon*. This division of the genera into two groups on the basis of brain morphology has been repeated recently by Radinsky (1973) who found distinctions in the relative size and shape of the prorean gyrus and hence in the profiles of the frontal lobes of the brain between the species of *Canis* and *Vulpes*. Radinsky, however, found that species of *Dusicyon* were intermediate between these two genera in the shape and size of the prorean gyrus (defined as the dorsal part of approximately the anterior two-thirds of the frontal lobe: Radinsky, pers. comm., 1974).

Vulpes vulpes (L., 1758)

Common fox, red fox

DISTRIBUTION. The common fox is the most widespread of all wild canids and even exceeds the wolf in its distribution. It is found in wooded and open country throughout the Palaearctic region, including North Africa, and in southeastern Asia, northern Indo-China and much of North America. The natural range has been extended by human agency, perhaps most notably into Australia.

DESCRIPTION. The largest member of the genus but very variable in size, as in many other characters, throughout its wide range. Typically the pelage is a rich rufous colour. The backs of the ears are black or dark brown and contrast strongly with the head and neck. There may be a black patch or mask between the nose and eyes. The insides of the ears are light in colour as are the chin and underparts. The tail, or 'brush', is very long and bushy and has a white tip. There is a dark stripe down the front of the foreleg, and the hindleg is black from the hock downwards. There are, however, many variations to this coat colour pattern and a melanistic form is quite common. A black and silver-grey variety (the silver fox) is bred in captivity for its fur.

The skull is one of the largest in the genus *Vulpes*, with a long narrow palatine region. An interparietal crest may be present but is not normally strongly developed. The temporal ridges lie close together. The cheek-teeth are sharp but rather small. P^2 and P^3 have no posterior secondary cusps. The canines are long and finely pointed.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes bengalensis	87·4	*Vulpes velox*	91·8
Vulpes velox	86·5	*Vulpes bengalensis*	91·4
Vulpes rueppelli	86·3	*Vulpes corsac*	90·2
Vulpes chama	84·9	*Alopex lagopus*	89·6
Vulpes corsac	84·5	*Vulpes chama*	89·2

Although *Vulpes vulpes* is the type species of the genus it bears a rather low similarity to the rest of the foxes on all characters (discussed in the section on typicalities, see p. 136), and on the two-dimensional plots it can be seen to be hardly less peripheral than *Alopex lagopus*, *Vulpes cinereoargenteus* and *Vulpes zerda* (Figs 2a, 3a, 5a). On cranial and dental characters, however, the common fox does lie well within the genus.

REMARKS. The common fox would undoubtedly have been domesticated by man if its solitary nature and pungent smell had not made it so intractable, for the species has had an almost symbiotic relationship with man since the prehistoric period. Fox bones are commonly found amongst Neolithic animal remains, especially in Western Asia (Clutton-Brock, 1969) where foxes appear to have been an important source of meat. Their pelts remain of economic value at the present day in many parts of the world. On the other hand, since the beginnings of livestock husbandry the fox has preyed on domestic animals and scavenged for food around homesteads. Attempts to control the fox's depredations on livestock have developed into one of the most highly ritualized of sports. Paradoxically, hunting of the fox has been the means, not only of its preservation, but also of an increase in its distribution. Before the emigration of Europeans to North America, the common fox may have had a much more restricted distribution over the whole continent, for it is known that foxes were imported into the eastern regions in the seventeenth century (Gilmore, 1946). British foxes were introduced by a hunt club into Australia in 1868 (Troughton, 1957).

Vulpes corsac (L., 1768)

Corsac fox

DISTRIBUTION. Steppe-lands of southeastern Russia, Volgo-Ural steppes, Russian Turkestan and Kirghizia, to Chinese Turkestan, Mongolia and Transbaikalia. Possibly also Manchuria and Northern Afghanistan (Ellerman & Morrison-Scott, 1966).

DESCRIPTION. A small fox, similar in size to *Alopex lagopus*, but with relatively longer legs. The fur is thick, soft and pale straw-coloured with darker, slightly tawny markings along the back. Except for a small black patch over the tail gland and a slightly black tip to the tail there is no dark colouring on the head, body or limbs. The underparts are pale. The three specimens in the British Museum (Natural History) have closely similar markings and Ognev (1962) described the same pelage characters. According to Ognev, this fox is less solitary than most species and may hunt in small packs. It feeds on rodents, birds, small reptiles and insects. Like *A. lagopus* the corsac fox may inhabit communal breeding dens.

Skull similar to that of *A. lagopus* but the teeth may be relatively smaller. The temporal ridges are flat and may enclose a lyriform sagittal area.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes bengalensis	93·7	*Alopex lagopus*	90·8
Vulpes velox	93·3	*Vulpes bengalensis*	90·7
Dusicyon gymnocercus	90·9	*Vulpes vulpes*	90·2
Vulpes ferrilata	89·8	*Vulpes velox*	90·0
Dusicyon vetulus	89·8	*Vulpes chama*	88·8

As shown by the 'near neighbours' tables the corsac fox lies closest to *A. lagopus* on cranial and dental characters and closest to *Vulpes bengalensis* on all characters. Phenetically the species is a typical fox, despite its small size and on the two-dimensional plots it lies within the *Vulpes* group.

Vulpes ferrilata Hodgson, 1842

Tibetan sand fox

Distribution. High plateau country of Tibet and Nepal between 4500 and 4800 m (Ellerman & Morrison-Scott, 1966 ; Pocock, 1941).

Description. The skins of this apparently rare fox have been described in some detail by Pocock (1936). The body colour is pale grey agouti or sandy with a tawny band along the dorsal region. The fronts of the legs are also tawny ; the underparts pale. Insides of the ears white, the outsides similar in colour to the rest of the body. The fur is soft and thick and the tail bushy. The end of the tail is white, whilst the anterior part has a wide band of dark guard hairs. There may be a dark streak over the tail gland. Very little is known of the habits of this fox or of the functions of its extraordinarily long head.

Skull peculiarly elongated and with a very narrow maxillary region. Canine teeth also remarkably elongated and pointed. Cheek teeth well developed but widely spaced in the long jaws. Mandible correspondingly elongated and with relatively little depth. Temporal ridges of the cranium flat and enclosing a narrow, lyriform sagittal area.

Systematic position. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Vulpes corsac	89·8	*Vulpes corsac*	88·4
Dusicyon gymnocercus	89·2	*Vulpes velox*	88·0
Dusicyon culpaeolus	89·1	*Dusicyon gymnocercus*	84·9
Dusicyon australis	88·9	*Vulpes chama*	84·8
Vulpes velox	87·9	*Dusicyon microtis*	82·7

Vulpes ferrilata is phenetically closer to the species of *Dusicyon* than is any other member of the genus *Vulpes*. Despite the unique appearance of the skull, however, it is of interest that in both near-neighbours tables this fox is slightly closer to *Vulpes corsac* than it is to any other species. The distribution of *V. corsac* lies to the north of that of *V. ferrilata* and it may be that the Tibetan fox has evolved from the more typical *V. corsac* in response to a specialized environment. An analogous situation may have occurred with *Canis simensis* which is phenetically close to *Canis adustus* and has a somewhat similar elongated muzzle.

Vulpes bengalensis (Shaw, 1800)

Bengal fox

Distribution. Open country, thorny scrub or semi-desert areas in southern peninsular India, Travancore, northwards to Sind, Bihar and Orissa, Kangra in Punjab, Haldibari and Nepal up to 1350 m (Ellerman & Morrison-Scott, 1966 ; Pocock 1941).

Description. This Indian fox is medium-sized and sandy-coloured with soft fur that is not as thick or long as it is in *Alopex lagopus* or *Vulpes corsac*. The dorsal region of the pelt may be darker or more tawny than the rest which is either pale agouti or fawn, with tawny legs. The insides of the ears are white, the outsides grey, and the underparts are light-coloured or pale ginger. The black tip to the tail is the only dark colouring in the pelage except that in a few specimens there is a small dark patch over the tail gland. Feeds on small animals, including insects, and eggs as well as a fairly high proportion of fruit and berries.

Skull typically 'fox-like', with long sharply pointed canines and well-developed molar teeth. The temporal ridges are flat and may enclose a lyriform sagittal area.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes velox	94·5	*Vulpes chama*	94·9
Vulpes chama	93·8	*Vulpes rueppelli*	92·3
Vulpes corsac	93·7	*Vulpes velox*	91·7
Vulpes rueppelli	93·3	*Vulpes pallida*	91·4
Dusicyon gymnocercus	91·9	*Vulpes vulpes*	91·4

The Bengal fox has a similarity of over 90 with other species of fox shown in the table above and as can be seen from Table 2, it is the 'most typical' member of the genus for the 'all-character' results and is only three below *Vulpes chama* for the skull characters. It is reasonable therefore to assume that *Vulpes bengalensis* typifies the 'basic fox'.

Vulpes cana Blanford, 1877

Blanford's fox

DISTRIBUTION. Not well known but probably the mountain areas of Kopet Dag, southwestern Russian Turkestan, Afghanistan, northeastern Iran and Baluchistan (Ellerman & Morrison-Scott, 1966; Ognev, 1962).

DESCRIPTION. A small fox with extremely soft fur and a long very bushy tail. The colouring is a blotchy black, grey and white with a dark tip to the tail and a dark patch over the tail gland. There is an almost black mid-dorsal line and the hind legs may be dark. Blanford (1888) described the pelt as having a 'rufescent tinge' but the skins examined in the British Museum appear to have no red pigment in the hair (see Table 6). The underparts are almost white; the ears are grey, and there is a small dark patch between the eyes and nose.

The condylo-basal length of the skull exceeds that of *Vulpes zerda* (the smallest species of canid) by only a few millimetres. Despite its small size the skull and dentition are typically vulpine with small sharply pointed teeth, flat temporal ridges and a narrow maxillary region.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes rueppelli	85·5	*Vulpes zerda*	89·5
Vulpes bengalensis	84·6	*Vulpes velox*	88·1
Vulpes velox	84·3	*Vulpes chama*	87·6
Vulpes zerda	83·4	*Vulpes rueppelli*	87·0
Vulpes chama	83·0	*Vulpes pallida*	87·0

The numerical results show a rather low similarity for this species with the rest of the genus *Vulpes*. On the two-dimensional plots, however, *Vulpes cana* lies close to the sand foxes and its phenetic relationships must be with this group.

Vulpes rueppelli (Schinz, 1825)

Sand fox

DISTRIBUTION. Arid areas of North Africa, southern Arabia, Persian Baluchistan and Afghanistan (Ellerman & Morrison-Scott, 1966 ; Harrison, 1968).

DESCRIPTION. A large-eared, desert, sand fox. The pelage is reddish-grey agouti with dark guard hairs on the tail and a dark patch between the eyes and nose. Light underparts. Ears not distinct in colour from the rest of the body. As with the other desert foxes, *Vulpes pallida* and *Vulpes zerda*, the facial vibrissae are particularly long and black.

Skull small but typically vulpine with a straight profile, narrow maxillae and small sharp canine teeth. Bullae large but not so expanded as in *V. zerda*.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Vulpes bengalensis	93·3	*Vulpes bengalensis*	92·3
Vulpes chama	91·1	*Vulpes chama*	90·9
Vulpes velox	91·1	*Vulpes velox*	89·8
Dusicyon culpaeolus	88·9	*Vulpes pallida*	89·6
Vulpes corsac	88·7	*Dusicyon gymnocercus*	87·1

Vulpes rueppelli is a small fox that is well adapted to life in dry sandy environments but it does not have the extreme desert-characters that are seen in *V. zerda*. The 'near-neighbours' tables and two-dimensional plots show that the species is phenetically close to *Vulpes bengalensis* and to the desert foxes (described in the following sections).

Vulpes pallida (Cretzschmar, 1826)

Pale fox

DISTRIBUTION. Dry sandy areas in a line running across Africa from Senegal through Nigeria and Cameroun to the Sudan and Somalia (Allen, 1939 ; Ellerman & Morrison-Scott, 1966).

DESCRIPTION. A small ginger-coloured fox with large ears that are the same colour as the body. The tail is dark and has a black tip and a dark patch over the tail gland. The underparts are pale and may be a pinkish ginger. Legs rufous. No dark patch between the eyes and nose.

Skull small with a wide lyriform sagittal area and a relatively short maxillary region. The upper molars are well developed in relation to the carnassial teeth (P^4) which are weak.

Systematic position. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes chama	92·4	*Vulpes chama*	95·2
Dusicyon sechurae	91·0	*Vulpes bengalensis*	91·4
Dusicyon fulvipes	90·9	*Vulpes rueppelli*	89·6
Vulpes bengalensis	90·5	*Vulpes velox*	89·0
Dusicyon gymnocercus	90·0	*Vulpes cana*	87·0

The systematic position of *Vulpes pallida* was discussed by Thomas (1918) in a short note on the sand foxes of North Africa. Thomas associated *V. pallida* with *Vulpes rueppelli* and *Vulpes zerda* and this grouping has been generally followed since then. Our numerical analysis of the phenetic characters suggests that these desert foxes are more closely related to the Indian fox *Vulpes bengalensis* and to the South African *Vulpes chama* than had been previously realized. The situation can be seen best as a series of species ranging in an arc from *V. chama* through *V. pallida, V. zerda* and *V. rueppelli* to *V. bengalensis*, with *V. zerda* as the most highly specialized desert form.

Vulpes cana (Blanford's fox) falls geographically within this arc, but it is adapted to a montane rather than a desert environment and its unusual pelage characters set it apart from the rest of the series.

Vulpes zerda (Zimmermann, 1780)

Fennec fox

Distribution. Desert areas of Morocco, Algeria, Libya, Egypt and east to Sinai and Arabia. Also south to the Sudan (Ellerman & Morrison-Scott, 1966; Harrison, 1968).

Description. The smallest species of canid, with extraordinarily large ears. The pelage has no agouti hairs but is an evenly pale fawn colour with almost white underparts. The tail tip is dark and there is a dark patch over the tail gland; these being the only parts of the body that are not pale in colour. There may be a ginger line along the back. The facial vibrissae are very long.

Skull very small with exceedingly large swollen bullae. Otherwise typically vulpine, except that the cranium is rather rounded and the dentition is weak. The sagittal area, enclosed by barely perceptible temporal ridges, is very wide.

Systematic position. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes chama	89·7	*Vulpes cana*	89·5
Vulpes pallida	88·9	*Vulpes pallida*	86·9
Vulpes bengalensis	88·5	*Vulpes bengalensis*	85·9
Dusicyon fulvipes	88·0	*Vulpes chama*	85·2
Vulpes velox	87·7	*Vulpes rueppelli*	83·7

V. zerda has been traditionally placed in a separate genus, *Fennecus*, and this classification is generally followed on account of this fox's huge ears, pale colouring and rounded skull. These characters should be seen, however, in their true context as adaptations to a most specialized environment. Like *Alopex lagopus* the fennec lies on the periphery of the fox group because it is adapted to extreme conditions where the biotic abundance is very low.

Table 3 shows that the fennec fox lies above *Vulpes ferrilata*, *Vulpes vulpes* and *Vulpes cana* in order of typicality and in the 'near neighbours' table it is seen to have similarity values of nearly 90 with the other small species of fox. The two-dimensional plots and centroid linkage dendrograms also show that the fennec lies well within the genus, more so than *V. vulpes*. It would therefore be irrational for us to exclude this species and although it makes for nomenclatural difficulties (see p. 150) we are constrained to transfer it to the genus *Vulpes*.

Vulpes chama (A. Smith, 1833)

Cape fox

DISTRIBUTION. Dry areas of southwestern Africa, Transvaal and possibly western Rhodesia. Probably extinct in the Capetown area (Allen, 1939; Ellerman *et al.*, 1953).

DESCRIPTION. A relatively large fox, similar in size to *Vulpes bengalensis*. The fur is soft and short and the colouring of the body is rufous agouti. There may be long black guard hairs on the bushy tail and on the posterior dorsal region. The tail has a distinct black tip and there is a diffuse dark patch over the tail gland. The underparts are a pale rufous with a lighter chin. The legs are more tawny than the general body colour. There is no dark mark between the eyes and nose.

Skull very similar to that of *V. bengalensis*, but the cranium is slightly wider and the maxillary region slightly shorter (see Table 4).

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes bengalensis	93·8	*Vulpes bengalensis*	95·2
Vulpes pallida	92·4	*Vulpes pallida*	94·9
Dusicyon culpaeolus	92·2	*Vulpes velox*	92·6
Vulpes velox	92·0	*Vulpes rueppelli*	90·9
Dusicyon gymnocercus	91·3	*Dusicyon sechurae*	89·8

The numerical results show that *Vulpes chama* is surprisingly closely related in its phenetic characters to the Bengal fox, *V. bengalensis*, and to the more northerly African fox, *Vulpes pallida*. On skull characters *V. chama* heads the list as the most typical member of the genus (Tables 2, 3) and as described under the description of *V. pallida*, it seems clear that this South African fox should be considered as one end of an arc of related species that have evolved in response to varying degrees of desert conditions.

Vulpes velox (Say, 1823)

Kit fox

For the purposes of this analysis *Vulpes macrotis* Merriam, 1888 was included within the species *Vulpes velox.*

DISTRIBUTION. Prairies of western North America. Distribution not well known but certainly decreasing. The northern subspecies is classed as endangered by the *Red data book* (Goodwin & Holloway, 1972) ; it is extinct in Canada.

DESCRIPTION. A medium-sized fox with very thick soft underfur and long agouti guard hairs. The body colouring may be tawny or light ochreous and grey. Tail relatively short and very bushy with a black tip and a slight black patch over the tail gland. There is a dark patch between the eyes and the nose. Large ears white inside and grey or ochreous outside. Almost white underparts. Limbs tawny.

Skull typically 'fox-like' and very similar to that of *Vulpes chama* and *Vulpes bengalensis.* Upper molar teeth slightly less well developed than in the latter species. Temporal ridges flat and enclosing a narrow lyriform sagittal area.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Vulpes bengalensis	94·5	*Vulpes chama*	92·6
Vulpes corsac	93·3	*Vulpes vulpes*	91·8
Vulpes chama	92·0	*Vulpes bengalensis*	91·7
Vulpes rueppelli	91·1	*Vulpes corsac*	90·0
Dusicyon culpaeolus	90·5	*Vulpes rueppelli*	89·8

It is clear from the results of this analysis that the phenetic affinities of *V. velox* lie with the 'most typical' members of the genus, these being *V. bengalensis* from India and *V. chama* from South Africa. On the other hand, the similarity of 91·8 that the skull of *V. velox* bears to that of *V. vulpes* may provide a link between this widespread but somewhat discrepant species and the more typical group. Support for this may be seen in the work done by Creel *et al.* (1971, 1974) on hybridization between the kit fox and the common fox.

Vulpes cinereoargenteus (Schreber, 1775)

Grey fox

DISTRIBUTION. Widespread in wooded country and along river valleys throughout Central and North America and the northern part of South America but not in the high plains (Cabrera, 1958 ; Hall & Kelson, 1959 ; Miller & Kellogg, 1955). A versatile carnivore that will easily adapt from a wooded to a pastoral environment (Hershkovitz, 1972 : 372).

DESCRIPTION. A medium-sized, typically 'fox-like' canid. Body colour grey agouti with white jaws and throat. Ears and sides of neck ochreous or tawny.

Chin grey or brown ; underparts pale ; legs and feet tawny. Long bushy tail. A dorsal black stripe extends from the mid-line of the back along the whole of the tail to the tip which is black. Hildebrand (1952b) stated that the tail gland is longer in this species than in any other canid. The gland is covered by a ridge of stiff guard hairs. (This character was used by Gray (1868) to support his classification of the grey fox in the separate genus *Urocyon* Baird, 1857.) Feeds on the usual small animals and birds that all foxes prey upon. The grey fox is said readily to climb trees to escape from hunters or other enemies – a most unusual habit for a canid.

Teeth well developed. Canines not as long as is typical for the fox group as a whole, and the premolars high-crowned in relation to their length. Carnassial and molar teeth 'fox-like'. The cranium is distinctive and similar to that of *Otocyon megalotis* in having the temporal ridges well developed but separated by a wide sagittal area. The surface of the parietal bones is rugose, whilst that of the sagittal area is smooth. The frontal sinuses are present only as barely visible pockets (in a bisected skull) below the postorbital processes. There is a subangular lobe on the mandible but it is not so well developed as in *O. megalotis*.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Vulpes bengalensis	89·5	*Vulpes pallida*	85·5
Vulpes velox	87·8	*Vulpes chama*	85·1
Vulpes corsac	87·8	*Vulpes rueppelli*	84·9
Vulpes rueppelli	87·6	*Vulpes velox*	83·5
Vulpes pallida	87·5	*Vulpes bengalensis*	83·3

A second species of grey fox, usually described as *Urocyon littoralis* Baird, 1858, is an island form that is probably closely linked to the mainland species. It has not been included in this analysis.

The systematic position of the grey fox has been one of the most interesting problems to emerge from the present analysis. There has been little work done on the affinities of the species in the past although both Huxley (1880) and Guilday (1962) have observed the similarity in skull conformation between the grey fox and *O. megalotis*.

The separation of the grey fox in the genus *Urocyon* is generally accepted, and it has been asserted since the time of Mivart (1890) that this fox has more in common with the South American canids (genus *Dusicyon*) than with the common fox (*Vulpes vulpes*), the only member of the fox group with which it has been compared by mammalogists. The misconception has arisen, in part, because of the atypical appearance of the common fox in comparison with the rest of the genus, and it may also stem from the work of Osgood (1934) who described the grey fox in his paper on the South American canids and, by implication, clearly thought of it as belonging to the South American group. He made no mention of any possible relationship of the species with *Vulpes*, and inferred that *Vulpes cinereoargenteus* was more closely related to *Dusicyon* than was *Chrysocyon brachyurus*, the maned wolf, a theory for which this analysis gives no support at all. It can, in fact, be asserted that the grey fox bears less phenetic resemblance to the South American genera of canids than do most other members of the family, and it can be shown, for the first time, that there is a considerable similarity (almost 90 per cent for all characters) between the grey fox and the typical *Vulpes bengalensis*. Furthermore *V. cinereoargenteus* has no similarity with any genus other than *Vulpes* in the 'near neighbours' tables.

The development of the temporal ridges and subangular lobe of the mandible do place the skull apart from all other members of *Vulpes* but within the terms of this numerical taxonomy it would not be consistent to keep the grey fox as a separate genus. It lies on the periphery of the *Vulpes* group, as can be seen from the two-dimensional plots, but less so than *V. vulpes* or *V. ferrilata*.

The southerly distribution of *V. cinereoargenteus* in relation to its phylogenetic origin has been much discussed. Most authors (including Mivart, 1890) have agreed that it must be a latecomer to South America. Hershkovitz (1972 : 312) described the species as a 'varicant', straddling the Nearctic and Neotropical regions and not clearly derived from either. He postulated further (p. 359) that the grey fox may have originated in Middle America and spread during the Quaternary into Canada and South America.

Now that the species has been critically examined in relation to all the other members of the canid family it may be said that derivation from *Dusicyon* or an autochthonous origin in Middle America seems unlikely. It appears that it has closer phenetic links in the Asiatic species of *Vulpes* than was previously suspected and perhaps it has been pushed south as a result of competition with the other canid species in North America, and in particular the highly successful *V. vulpes* which was probably aided in the extension of its range by the activities of man (see p. 153).

Genus ***ALOPEX*** Kaup, 1829

One species.

Alopex lagopus (L., 1758)

Arctic fox

Distribution. Arctic tundra of Europe, Asia and North America and areas of montane tundra in Scandinavia. In Asia southwards to Kamchatka (Ellerman & Morrison-Scott, 1966 ; Macpherson, 1969).

Description. A small compact fox. The pelage is distinct in that it has two colour phases. One phase is pure white in winter, whilst in summer the back, legs, tail and head are dark brown and the underparts are light. The other phase is described as 'blue' and is more variable, being grey, brown or black in summer and winter. The fur is thick and very soft with guard hairs as fine and long as the underfur. Muzzle and ears relatively short, tail very thick and bushy. The Arctic fox is solitary in its hunting habits but the breeding dens are often found in colonies.

Skull rather shorter in the palatine region than in *Vulpes vulpes* and the frontal bones are slightly swollen at their junction with the nasals, but this does not affect the depressions on the postorbital processes which are characteristic of the genus *Vulpes*. Dentition as in *V. vulpes* but the canines may be relatively shorter.

The Arctic fox feeds on small mammals, especially lemmings (*Dicrostonyx* and *Lemmus* spp.) and carrion. When lemmings are scarce the fox will feed more heavily on birds' eggs, insects, berries and other fruits and seeds.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Vulpes pallida	81·6	*Vulpes corsac*	90·8
Vulpes chama	81·5	*Vulpes vulpes*	89·6
Vulpes corsac	81·2	*Vulpes rueppelli*	86·7
Dusicyon gymnocercus	81·0	*Vulpes bengalensis*	86·3
Dusicyon culpaeolus	80·7	*Dusicyon culpaeolus*	85·2

Up to the present time the Arctic fox has been commonly classified in a separate genus, *Alopex* Kaup, 1829, although some authors, including Bobrinskii (1965), have preferred to make *Alopex* a subgenus of *Vulpes*. Miller (1912, p. 318) listed the following distinctive characters in support of separate generic status: 'Skull intermediate in general form between that of *Canis* and *Vulpes*; occipital depth about one third condylo-basal length; interorbital region more elevated than in *Vulpes*; postorbital processes thin, flat, or slightly concave above, with bead-like overhanging edges; dorsal profile of forehead rising abruptly above rostrum as in *Canis*; teeth moderately heavy and large; external form fox-like, but ear short and rounded, not conspicuously overtopping the surrounding fur.' Miller went on to state that although in most respects intermediate between *Canis* and *Vulpes* the Arctic foxes form such a natural group that they should be in a distinct genus.

When the skull of the Arctic fox is compared with that of *Vulpes vulpes* most of the above distinctions can be seen to hold, although we have not noticed any difference in the degree of depression in the postorbital processes in *Alopex lagopus*. When the skull is compared with that of *Vulpes corsac*, however, there are fewer differences and as can be seen from the 'near neighbours' table, *A. lagopus* has a similarity of 90 with the skull of this species.

Alopex lagopus is a species of fox that has special adaptations to life in an arctic environment where there is low biotic abundance, and although the skull is similar to that of *V. corsac*, on the numerical results for all characters the species is separated at a similarity of only just over 80. It is clear from the two-dimensional plots that the Arctic fox lies close to the genus *Vulpes* but its inclusion amongst the foxes in the table of 'typicality' (Table 3) shows that it is the most aberrant of the foxes and there are therefore grounds for retaining it in a separate genus.

Genus ***OTOCYON*** Muller, 1836

One species.

Otocyon megalotis (Desmarest, 1822)

Bat-eared fox

DISTRIBUTION. Arid areas in South Africa, southern Angola, Botswana, perhaps western Rhodesia, East Africa and northwards to the Sudan, Ethiopia and Somalia (Ellerman *et al.*, 1953).

DESCRIPTION. A long-legged, medium-sized fox with very large, wide ears, long fur and a very bushy tail. The general colour is brownish or ochreous with grey agouti guard hairs. Throat, underparts and insides of ears pale. Limbs nearly black as are the outsides of the ears and the muzzle. Black tip to the tail. Omnivorous, social animals, living in groups and feeding on insects, small rodents, fruit and berries. Adapted to life in a desert environment.

Apart from the dentition the skull bears a singular resemblance to that of *Vulpes cinereoargenteus*, with well-developed temporal ridges enclosing a wide sagittal area and rugose parietal bones that contrast with the smooth surface of the sagittal area. Bullae large. No frontal sinuses. Dentition unique in that there are always at least three upper and four lower molar teeth. Carnassials much reduced in length. Canines large and 'fox-like'. Premolar teeth high-crowned in relation to their length as in *V. cinereoargenteus*. Subangular lobe of the mandible unusually large. Basal line of the horizontal ramus very straight.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Vulpes chama	75·6	*Vulpes cinereoargenteus*	75·9
Vulpes vulpes	73·4	*Vulpes pallida*	67·1
Vulpes pallida	72·7	*Nyctereutes procyonoides*	66·0
Vulpes cinereoargenteus	72·6	*Vulpes rueppelli*	65·6
Vulpes velox	72·0	*Vulpes vulpes*	65·6

Huxley (1880) suggested that *Otocyon megalotis* was the most primitive member of the canid family and that its extra molar teeth represented the basic mammalian dentition. Matthew (1930 : 123) believed that 'an extra upper and lower molar had appeared', but he gave no further explanation of this appearance. Guilday (1962) put forward the theory that the extra teeth were the result of a mutation that duplicated the upper first and lower second molars at the expense of the carnassial teeth which were correspondingly shortened in length. This theory seems sound, for the molars in question are most similar to each other. That this mutation is of considerable age is shown by the finding of a primitive *Otocyon* in the Villafranchian of Olduvai, Tanzania. This specimen was named *Protocyon reckii* by Petter (1964) who considered it to be more primitive than the Recent form and ancestral to it. Simpson (1945 : 224) tentatively allowed the subfamily rank of Otocyoninae Trouessart, 1885 to stand for this monotypic genus but it is clear that he did not really approve of it. Our numerical results support Simpson's hesitation and there seems little doubt that *O. megalotis* should be considered as an aberrant fox with affinities to *Vulpes cinereoargenteus*. There is therefore no justification for the recognition of a subfamily Otocyoninae, but the generic status of *Otocyon* is clearly established by the low level of similarity that it bears to all other species. The similarities in behaviour between *O. megalotis* and *Nyctereutes procyonoides* are discussed in the next section.

Genus ***NYCTEREUTES*** Temminck, 1839

One species.

Nyctereutes procyonoides (Gray, 1834)

Raccoon dog

DISTRIBUTION. River valleys and the edges of forests in the Amur and Ussuri region of eastern Siberia, Japan, Manchuria, China and Indo-China (Ellerman & Morrison-Scott, 1966 ; Ognev, 1962). Introduced and now widespread in European Russia and eastern Europe.

DESCRIPTION. A rather slow-moving, heavy-bodied canid with a small head and short limbs. The pelage characters give it a superficial resemblance to the raccoon, *Procyon lotor* (L.). The back is a mottled tawny and black, the guard hairs being long, banded, rather coarse and shiny ; the underfur is abundant, soft and fawn in colour. The tail is rather short and dark at the end but without a distinct black tip. Limbs fawn or dark brown. The facial region is short. The raccoon dog is the only species of canid that has a distinct dark mask around the eyes and between the eyes and ears. Beneath each eye there is a diffuse white band stretching back to the ears and emphasizing the dark mask. Underparts brown, beige or fawn. Nocturnal, fossorial, hunting in pairs or family groups. Preferred habitat, small forested areas near water, and river valleys. Diet very varied : often eats fish and feeds on small rodents, amphibians, eggs, shellfish, berries and acorns (Ognev, 1962). Hibernates.

Skull small with short nasals and maxillary region. Distinct subangular lobe to the mandible but not so highly developed as in *Otocyon megalotis*. Teeth small and weakly developed. Molars somewhat bunodont. Palatine bones extend backwards beyond M^2. Surface of parietal bones rugose. Temporal ridges fused to form a slight interparietal crest. Orbits relatively small. Frontal sinuses moderately large.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Dusicyon microtis	78·1	*Dusicyon sechurae*	86·2
Dusicyon australis	77·4	*Canis aureus*	83·5
Dusicyon thous	76·8	*Dusicyon australis*	83·2
Dusicyon vetulus	76·4	*Alopex lagopus*	82·9
Dusicyon sechurae	75·7	*Vulpes cinereoargenteus*	82·2

It is difficult to assess the systematic position of *Nyctereutes procyonoides* as it has no close affinities with any of the other canids. The 'near neighbours' tables place the genus at a low level of similarity with the *Dusicyon* group and in this context it may be mentioned that in 1880 Huxley wrote, in his study of the Canidae: '*Nyctereutes* is essentially a low Thooid of the South American type.'

Radinsky (1973) has suggested on the basis of the shape of the prorean gyrus of the brain that the raccoon dog should be linked with the foxes. The presence of fairly well-developed frontal sinuses in the skull does not, however, lend support to this view. Kleiman (1967) in her study of some aspects of the behaviour of the Canidae asserted that *Nyctereutes* is unique in that a submissive animal does not wag its tail. She noted several striking similarities between the raccoon dog and the bat-eared fox (*O. megalotis*). Both engage in communal sleeping and social grooming which she says may be related to the black facial mask that is present in both species although much more extensive in *Nyctereutes* where, as previously stated, it surrounds the eyes and goes back to the ears. Both species share a peculiar tail posture; in dominant animals or in a sexually aroused male the tail is carried in an inverted U-shape, and the black hair on the tail is erected and stands up prominently.

There can be little doubt about the generic status of *Nyctereutes*. On the two-dimensional plots and on the centroid linkage dendrograms the raccoon dog is always an outsider and it bears a similarity value of less than 75 with the genera *Canis*, *Vulpes* and *Dusicyon* (Table 1).

Genus **DUSICYON** Hamilton Smith, 1839

Type species *Dusicyon australis* (Kerr, 1792)

All the species within the genus *Dusicyon* are restricted to the continent of South America and its neighbouring southern islands. The number of taxa that we suggest should be included in the genus differs from that of the accepted check list of Cabrera (1958) which excludes *Dusicyon thous* and *Dusicyon microtis*. Of the eleven species that were examined for this analysis eight form a phenetically closely linked group and it is suggested that further work at the specific level might lead to the elimination of four of these. Three species, *D. australis*, *D. thous*, and *D. microtis* lie on the periphery of the group and their taxonomic position is discussed.

It is difficult to give a diagnosis for the genus as in many characters it lies between *Canis* and *Vulpes*, with *D. australis* presenting the most 'dog-like' features and *D. vetulus* the most 'fox-like'. An indication of this intermediate state is apparent in the descriptions of the early authors who wrote of the animals as 'foxes', 'wild dogs' or 'wolves'. Gray (1868) described them as 'fox-tailed wolves'.

The pelage is usually grey agouti with some ochreous or tawny colouring, with the exception of *D. microtis* which is dark all over. The ears are fairly large and erect; the head is rather narrow, and the tail is very long, bushy and has a contrasting dark tip (white in *D. australis*). The underparts are usually pale and the legs ochreous or tan. The skull is rather long and narrow with temporal ridges either apart and enclosing a lyriform sagittal area or nearly fused. There is no well-marked inter-parietal crest. Dentition is more 'fox-like' than 'dog-like'. The canines are long and finely pointed ; the premolars and carnassials are high-crowned, and the molars are well developed. The carnassial teeth are short relative to the lengths of the molars and to the condylo-basal length. The palatine bones may extend backwards beyond M^2.

Early writers on this group of South American canids usually placed them all within the genus *Canis* until the work of Thomas (1914) which brought the following generic names into common use : *Dusicyon* Hamilton Smith, 1839 ; *Cerdocyon* Hamilton Smith, 1839 ; *Pseudalopex* Burmeister, 1856 ; *Lycalopex* Burmeister, 1856.

Thomas designated the Falkland Island 'dog' (formerly known as *Canis antarcticus* Shaw, 1800) as the type of *Dusicyon.*

With the general acceptance of Pocock's paper (1913) on the affinities of the Falkland Island 'wolf', in which he allied this species closely with the other South American canids, Thomas's classification was followed, with minor alterations, by Kraglievich (1930) and Cabrera (1931). Osgood (1934) reduced *Cerdocyon, Pseudalopex* and *Lycalopex* to subgenera of *Dusicyon* and retained *D. australis* as *D.* (*Dusicyon*) *australis.* Simpson (1945) accepted this classification, but most recent authors have followed Cabrera's further modifications, in which he placed *D. thous* in the genus *Cerdocyon* and separated *D. microtis* into a new genus *Atelocynus* Cabrera, 1940, leaving the remainder as *Dusicyon.* Langguth (1970, 1975) went further and separated *Lycalopex vetulus* as an additional monospecific genus, while including the remaining species of *Dusicyon* in *Canis.*

The subgenus has been avoided throughout this work because of the absence of sufficiently discrete groups at the appropriate level. This being so, and after a careful examination of the numerical results, it has been decided to include all the genera and subgenera mentioned above within the genus *Dusicyon.*

Dusicyon australis (Kerr, 1792)

Falkland Island wolf

Although well known from the descriptions of Darwin and others, no detailed examination has been made of the available material of this extinct species since the account of Pocock (1913). It was therefore considered appropriate to give here a fresh description of the material that is held in the British Museum (Natural History) especially as there are many interesting features about the skulls and skins that make the systematic position of the species hard to define.

MATERIAL. No. 37.3.15.47. The holotype of *Dusicyon darwini* Thomas, 1914. Skull, mandible and skin from East Falkland Island. Collected by Charles Darwin and presented by Burnett and Fitz Roy. There are shot holes in the frontal bones behind the orbits and the occipital region of the skull is missing. Young adult male. Data on this specimen were used in the analysis.

No. 37.3.15.48. Skull, mandible and skin from West Falkland Island. Collected by Charles Darwin and presented by Burnett and Fitz Roy. Skull complete except for the left zygomatic arch which is missing. Young adult female. Data used in the analysis.

No. 69.2.24.3 (1692a). Skull without mandible; complete except for the right canine tooth which is missing. No history except that the skull was purchased from E. Gerrard, jun. It is, however, likely that this skull came from the live animal that was brought to the Zoological Gardens, London, by Mr A. A. Lecombe in 1868 (Newton, 1868). Young adult. This skull was not available at the time the numerical analysis was carried out but it agrees in every important respect with those specimens that were used.

No. 85.10.12.1 (1962b). Skull without mandible. North coast, West Falkland Island. Dentition and zygomatic arches incomplete. Presented by E. A. Holmsted. The skull had obviously lain in the sea for some time as it is covered with tiny barnacles. This could raise the possibility that it actually came from a domestic dog rather than from *Dusicyon australis*. The skull, however, has all the characters that are typical of the Falkland Island 'wolf' rather than of a domestic dog; these being the raised sagittal area and lack of interparietal crest, the extension of the palatine bones backwards from M^2, and the development of the malar bone (see Pocock, 1913). Data on this skull were included in the analysis.

No. 1974.483 (1692b). Left mandibular ramus with P_2, P_3, P_4, M_1. Although this mandible has the same number as the old registered number of the skull above (no. 85.10.12.1) it cannot be from the same animal as it is too large; nor does it fit the other skull with no mandible (no. 69.2.24.3). There is no history for this specimen and it is not recorded in the British Museum catalogues. It can be identified as *D. australis* on the unique character of the lower carnassial in which the little cusp (metaconid) at the base of the main cusp, on the lingual side of the tooth, lies only slightly above the inner cusp of the talonid. Data from this mandible have not been used in the analysis.

A further two skulls from the collection of the Royal College of Surgeons (nos 635 & 636) were described by Pocock (1913) and Thomas (1914) but unfortunately these have been missing since the 1939–45 war. These two skulls were catalogued as follows by Flower (1884): No. 635. Skull O.C. 4363. Presented by Admiral Sir Francis Beaufort. No. 636. Skull. Found by the donor on West Falkland Island. Presented by E. A. Holmsted, Esq., 1878.

DISTRIBUTION. Inhabited East and West Falkland Islands until about 1880 when the species became extinct.

DESCRIPTION. A 'large wolf-like fox' (Darwin, 1860) with a short face, wide muzzle and short ears. The tail short with a white tip. Coat thick and soft, mainly brown in colour with some rufous and speckled with white from pale guard hairs. Underparts pale, becoming cream at the posterior ventral surface. As remarked by Mivart (1890) and Pocock (1913) there is a dark reddish patch above the hock of the hind leg. The middle part of the tail has long dark guard hairs that contrast with the white tip. They fed mainly on birds, especially the upland goose, *Chloephaga picta*.

Skull large, with relatively wide palatine region. Temporal ridges well developed, enclosing a lyriform sagittal area which is flattened and only formed into an interparietal crest at the posterior end of the cranium. Enlarged frontal sinuses. No subangular lobe to the mandible. Palatine bones extend backwards beyond the posterior edge of M^2. Teeth large and somewhat compacted in the premolar region. Canines 'fox-like', premolars simple and high-crowned. P^4 with the protocone drawn backwards and reduced. Inner tubercle (metaconid) of M_1 placed very low, on a level with the posterior cusps (talonid), as figured by Pocock (1913 : 390).

The animals that inhabited the East Falkland Island were said to be larger and less red than those on the West Island. Hamilton Smith (1839) recorded a legend that the eastern group was descended from dogs left on the island by the Spanish, whereas the western group consisted of truly wild indigenous 'foxes'. Thomas (1914) examined the material in the British Museum and in the Royal College of Surgeons and decided that two species were represented. These he named *Dusicyon darwini* (eastern) and *Dusicyon antarcticus* (western).

Apart from there being some doubt about which island two of the skulls originated from, with Thomas altering 'west' to 'east' to suit his case, an examination of the four skulls and two skins now available shows a remarkable similarity between them. Aside from the variation in size that could be due to sex there are few differences in the skull that could be even ascribed to individuality. When Darwin visited the Falkland Islands in 1834 it was apparent to him that the wild 'foxes' that he saw there were doomed to extinction (Darwin & Waterhouse, 1840) and fifty years later they had indeed been exterminated. There remain, however, several contemporary accounts of the species, as well as the few specimens preserved in museums. The extinction of this species was due to indiscriminate slaughter and to the value of its fur to traders as far away as New York. The generic name of *Dusicyon* was given to this species by Hamilton Smith in 1839 after he had seen a large collection of pelts in a fur store in New York, owned by a Mr Astor. Hamilton Smith described these pelts as indistinguishable from those of *Lyciscus cagottis* (the Mexican coyote, *Canis latrans*).

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Vulpes ferrilata	88·9	*Canis mesomelas*	92·5
Canis aureus	88·8	*Canis aureus*	91·4
Dusicyon sechurae	88·6	Dingo	91·1
Dusicyon culpaeolus	88·6	*Canis latrans*	88·9
Dusicyon gymnocercus	87·7	*Dusicyon sechurae*	88·6

Pocock (1913) examined the skulls and skins of *D. australis* and decided that they bore a close affinity with *Dusicyon culpaeus* and that the species could be in no way a near relation of *Canis latrans*. Pocock was incited to pay attention to the Falkland Island 'wolf' by a quotation of Lydekker's from Huxley's work on the cranial and dental characters of the Canidae (1880). In this work Huxley concluded that *D. australis* was in some skull characters close to *C. latrans*.

The results of the present analysis support Huxley's observations in showing that the skull and teeth are closer to *Canis* than to *Dusicyon*. There are definite characters, however, like the length and shape of the canines that more closely resemble

Dusicyon, and the shape of the lower carnassial tooth is unique. So it will not be proposed here that the Falkland Island 'wolf' be returned to the genus *Canis*; the results are too uncertain and there is not enough material to make a thorough investigation possible. It may be remarked, however, that Pocock was somewhat hasty in his total rejection of Huxley's observations which in this, as in other parts of the work, are found to agree very well with the results obtained from our numerical analysis. In the two-dimensional plots as well as in the dendrogram for cranial and dental characters *D. australis* lies as close to, or closer to, *Canis* than to *Dusicyon* (Figs 2b and 8b).

The Falkland Islands lie within the continental shelf, approximately 400 km east of Patagonia (51–53° S, 57–61° W). It is possible that at some stages of the Pleistocene the islands were connected with the mainland and may have supported a mammalian fauna. If so, it could be argued that the canid became isolated on the islands when they became finally detached from the continent. It would be most surprising, however, for the only relic of a Pleistocene fauna to be one large carnivorous species. It seems much more likely that *D. australis* was taken to the Falkland Islands as a domestic animal by early man. This could have happened thousands of years ago, allowing the population to evolve into an autochthonous race, similar to the dingo. Support for this view is seen in the white tip of the tail (all other *Dusicyon* species have a black tip), the enlarged frontal sinuses and the wide muzzle when compared with other species of *Dusicyon*. These characters can signify domestication and frequently occur in the dingo.

If the Falkland Island 'wolf' was descended from domesticated animals it is perhaps possible that a species of *Dusicyon* was the progenitor rather than a species of *Canis*. Hamilton Smith (1839), amongst other early writers, described a domesticated form of *D. culpaeus* but he stated that the Indians preferred imported European dogs and that these were superseding the indigenous varieties.

Unless further evidence from fossil or archaeological sources comes to light, the origin of *D. australis* must remain speculative and although the results of this analysis show that the species was quite distinct from the mainland canids, the evidence does not justify giving it separate generic status.

Dusicyon culpaeus (Molina, 1782)

Colpeo fox

DISTRIBUTION. Widespread throughout the Andes mountains and hilly regions of the western and southern countries of South America up to 4000 m (the 'Patagonian subregion' of Hershkovitz, 1957, 1972; see also Cabrera, 1931, 1958; Langguth, 1970).

DESCRIPTION. Variable in size – can be large and 'wolf-like'. Head, neck, ears and legs tawny or rufous. Underparts pale. Back and shoulders grey with agouti (banded) guard hairs. Underfur fawn. Tail bushy with black tip; length over half that of the head and body combined.

Skull longer and narrower in the facial region than in *Dusicyon australis.* Frontal bones flat. Interparietal crest poorly developed. Palatine bones do not extend backwards beyond the posterior edge of M^2. Canines and premolars simple and 'fox-like' as in *D. australis.* The metaconid of M_1 higher than the level of the talonid as is usual in the Canidae.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Dusicyon gymnocercus	93·9	*Dusicyon inca*	88·5
Dusicyon culpaeolus	93·3	*Dusicyon gymnocercus*	88·1
Dusicyon inca	92·7	*Dusicyon culpaeolus*	87·5
Dusicyon griseus	92·7	*Canis simensis*	86·5
Dusicyon fulvipes	90·0	*Canis latrans*	86·1

The three species *Dusicyon culpaeus*, *Dusicyon gymnocercus* and *Dusicyon culpaeolus* are phenetically very close to each other. The pelage characters are so similar that it would be hard to define differences between them and perhaps the distinctions that have been found in the skulls may be attributable to individual variation. It is not possible, however, within the scope of this work to discuss problems of speciation and although it may appear from the numerical taxonomy that these three should be placed in one species they could be valid biological entities whose ecological distributions do not overlap.

Dusicyon culpaeolus (Thomas, 1914)

DISTRIBUTION. Uruguay (Cabrera, 1958).

DESCRIPTION. Very similar to *Dusicyon culpaeus*, but smaller. Considered by Kraglievich (1930) to be a subspecies of *Dusicyon gymnocercus* and it certainly bears the closest phenetic resemblance to this species.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Dusicyon gymnocercus	96·2	*Dusicyon gymnocercus*	95·3
Dusicyon inca	93·6	*Canis adustus*	92·0
Dusicyon culpaeus	93·3	*Dusicyon inca*	92·0
Canis mesomelas	92·9	*Canis mesomelas*	91·9
Dusicyon griseus	92·7	*Dusicyon fulvipes*	89·1

D. culpaeolus was not known as a separate species until the description of Thomas (1914) which was made from one skull and skin in the British Museum. Further examination might show that it should be included, with *D. gymnocercus*, in *D. culpaeus.*

Dusicyon gymnocercus (Fischer, 1814)

Azara's fox

DISTRIBUTION. Paraguay, northern Uruguay, southeastern Brazil and eastern Argentina (Cabrera, 1931, 1958).

DESCRIPTION. Like *Dusicyon culpaeolus* the phenetic characters of this species show close similarity to *Dusicyon culpaeus*, from which it differs only in the shorter, wider rostrum and more uniform pelage.

SYSTEMATIC DISTRIBUTION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon culpaeolus	96·2	*Dusicyon culpaeolus*	95·3
Dusicyon griseus	95·5	*Dusicyon griseus*	91·8
Dusicyon fulvipes	94·3	*Dusicyon fulvipes*	91·8
Dusicyon culpaeus	93·9	*Canis adustus*	91·5
Dusicyon inca	93·8	*Canis mesomelas*	90·7

Like *D. culpaeolus* this form may prove to be conspecific with *D. culpaeus*.

Dusicyon inca (Thomas, 1914)

DISTRIBUTION. Peru at 4000 m (Cabrera, 1958).

DESCRIPTION. A fairly large canid similar in size to *Dusicyon culpaeus* but distinguishable from it by a more evenly grizzled pelage. Tail with a distinct black tip. Chin black, ears and outer sides of legs a dull tawny brown. Underparts brownish white.

Skull similar to that of *D. culpaeus*.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon gymnocercus	93·8	*Dusicyon culpaeolus*	92·0
Dusicyon culpaeolus	93·6	*Dusicyon gymnocercus*	88·8
Dusicyon culpaeus	92·7	*Dusicyon culpaeus*	88·5
Dusicyon fulvipes	91·3	*Canis adustus*	88·3
Dusicyon griseus	90·3	*Canis mesomelas*	88·0

This is another of Thomas's species that was described from a single skull and skin (the type is in the British Museum), and like *Dusicyon culpaeolus* it is possible that a study of further material might show that it should be included with *D. culpaeus*. It should be pointed out, however, that the pelage of the one skin of *D. inca* in the British Museum is distinguishable from that species and in fact more closely resembles that of *Dusicyon griseus*.

Dusicyon griseus (Gray, 1836)

Argentine grey fox

DISTRIBUTION. The plains and low mountains of Patagonia, western Argentina and Chile (Cabrera, 1931, 1958).

DESCRIPTION. A small species. Ears large, head rust-coloured flecked with white. Agouti guard hairs with pale underfur giving a generally pale appearance to the back. Underparts pale grey. Feet tawny. Tail long and moderately bushy. The pelage of this species looks very like that of *Dusicyon fulvipes*, *Dusicyon inca*, *Dusicyon sechurae* and *Dusicyon vetulus* but (from the skins in the British Museum) it is less red than *D. fulvipes* and more red than the remaining species.

Skull small and 'fox-like' with faintly marked temporal ridges enclosing a wide lyriform sagittal area. Teeth widely spaced and 'fox-like'.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon gymnocercus	95·5	*Dusicyon fulvipes*	92·8
Dusicyon fulvipes	94·4	*Dusicyon gymnocercus*	91·9
Dusicyon culpaeolus	92·7	*Vulpes velox*	89·0
Dusicyon culpaeus	92·7	*Dusicyon culpaeolus*	87·9
Vulpes bengalensis	91·1	*Vulpes bengalensis*	86·9

The skull of *Dusicyon griseus* has little to distinguish it from that of *Dusicyon culpaeus* except for its small size and lack of interparietal crest (absence of a crest appears to be associated with small size in the Canidae).

Dusicyon fulvipes (Martin, 1837)

Darwin's fox, Chiloe fox

DISTRIBUTION. The southern part of the Island of Chiloe. This is one of the very many islands that lie off the coast of Chile between latitudes 40–45°, separated from the mainland by a narrow channel, the Gulf of Corcovado.

DESCRIPTION. Smaller than *Dusicyon griseus* with a uniformly dark and rufous pelage. The ears, head and legs are tawny, the back dark grey with agouti guard hairs. The tail is neither long nor bushy but has a black tip.

Skull as in *D. griseus* but smaller.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon griseus	94·4	*Dusicyon griseus*	92·8
Dusicyon gymnocercus	94·3	*Dusicyon gymnocercus*	91·8
Dusicyon sechurae	93·1	*Cerdocyon thous*	90·0
Dusicyon culpaeolus	92·7	*Dusicyon culpaeolus*	89·1
Dusicyon inca	91·3	*Vulpes chama*	89·0

It appears that this canid has always been somewhat rare or otherwise very shy and not many specimens have been collected. Osgood (1943 : 72) described how he trapped a pair of adults on the beach in 1922. These two were very similar in pelage characters and skull conformation to Darwin's specimen. Osgood stated that there is a close agreement in characters between *Dusicyon fulvipes* and *D. griseus* and suggested that Darwin's fox is merely an island form of *D. griseus* rather than a separate species. The results of this analysis support Osgood's suggestion.

REMARKS. The type specimen of this species was collected by Darwin and the skull and skin are now in the British Museum (no. 55.12.24.431) together with one other skull and skeleton (no. 51.11.8.4 (996a) purchased from Mr Brandt). The identification of this second specimen is not certain, however, because the original entry in the catalogue has the word 'Chili', and there is no indication that the animal came from the Island of Chiloe. The following account of the 'fox' that Darwin collected may be quoted from his *Voyage of the Beagle* (1860 : 280) :

> 'December 6th. 1834. In the evening we reached the island of San Pedro, where we found the Beagle at anchor. In doubling the point, two of the officers landed to take a round of angles with the theodolite. A fox (*Canis fulvipes*), of a kind said to be peculiar to the island, and very rare in it, and which is a new species, was sitting on the rocks. He was so intently absorbed in watching the work of the officers, that I was able, by quietly walking up behind, to knock him on the head with my geological hammer. This fox, more curious or more scientific, but less wise, than the generality of his brethren, is now mounted in the museum of the Zoological Society.'

Dusicyon sechurae (Thomas, 1900)

Sechura desert fox

DISTRIBUTION. The arid coastal zone of northwestern Peru and southwestern Ecuador, including the Sechura desert (Cabrera, 1931, 1958).

DESCRIPTION. A small light species with pale agouti guard hairs and fawn underfur. Cream to fawn underparts. Little or no rufous colouring on the body. Tail with distinct black tip.

Skull small with lyriform sagittal area and no interparietal crest. Palatine bones extend backwards beyond the posterior edge of M^2. Teeth small with 'fox-like' canines.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Dusicyon vetulus	94·5	*Dusicyon vetulus*	92·1
Dusicyon fulvipes	93·1	*Vulpes chama*	89·8
Dusicyon gymnocercus	92·6	*Dusicyon australis*	88·6
Vulpes pallida	91·0	*Dusicyon fulvipes*	88·5
Dusicyon culpaeolus	90·4	*Vulpes velox*	87·6

In pelage characters this species lies close to *Dusicyon griseus* and *Dusicyon vetulus*. Its small size may be an adaptation to desert conditions.

Dusicyon vetulus (Lund, 1839)

Hoary fox

Distribution. The most northeastern of the species of *Dusicyon* that have been described so far. Found in south-central Brazil, Minas Gerais and Mato Grosso.

Description. The smallest species of *Dusicyon*, similar in size to the smallest true foxes, for example *Vulpes pallida*. Pelage as for *Dusicyon sechurae* but with a marked dark stripe along the dorsal line of the tail.

Skull small with faintly marked temporal ridges, a very narrow lyriform sagittal area and a slight interparietal crest. Teeth small with widely spaced premolars and reduced upper carnassial (P^4). Canines sharply pointed and 'fox-like'. Anterior part of the frontal bones slightly swollen.

Systematic position. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Dusicyon sechurae	94·5	*Dusicyon sechurae*	92·1
Dusicyon gymnocercus	91·2	*Vulpes bengalensis*	86·0
Vulpes bengalensis	90·1	*Dusicyon australis*	85·4
Dusicyon fulvipes	90·0	*Vulpes chama*	85·2
Dusicyon griseus	89·9	*Canis mesomelas*	84·6

This species is noted for its small teeth and reduced carnassials which, combined with its somewhat isolated distribution in the central and eastern parts of the continent, have inclined previous authors to place it in a separate genus. The first description of the species was by Burmeister (1854 : 99) who created the genus *Lycalopex* for it. This was followed by Gray (1868) and by all subsequent authors until Osgood (1934) reduced *Lycalopex* to a subgenus of *Dusicyon*. Cabrera (1958) and Simpson (1945) accepted this change and this nomenclature has been in general use up to the present. Langguth (1970, 1975) has, however, reverted to classifying the species in a separate genus, that is, *Lycalopex vetulus*.

Although the two-dimensional plots show that *Dusicyon vetulus* lies somewhat on the edge of the *Dusicyon* group the analysis provides no evidence that the species should be separated at the generic level and for all phenetic characters it is clear that it lies very close to *Dusicyon sechurae*. The reduction in the size of the teeth may be more apparent than real for they are in proportion to the small size of the skull.

Dusicyon thous (L.)

Common zorro, crab-eating fox

Distribution. Savannah and woodland areas of northeastern South America, Columbia, Guiana, Brazil and south into northern Argentina (Cabrera, 1931, 1958 ; Hershkovitz, 1957 ; Langguth, 1970).

Description. A fairly small, dark canid with a grizzled-brown or grey pelage. The legs may be tawny, underparts brownish-white and ears ochreous or rufous. The tail is fairly long, bushy and either totally dark or with a black tip. Ears short. The caecum was said by Garrod (1873) to be nearly straight rather than convoluted as in most canids.

Temporal ridges faintly marked and enclosing a lyriform sagittal area. Frontal sinuses well developed and nasal bones slightly swollen in the facial region. Teeth large but canines not particularly long.

Systematic position. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon fulvipes	91·1	*Dusicyon fulvipes*	90·0
Dusicyon griseus	86·7	*Dusicyon gymnocercus*	88·4
Dusicyon microtis	86·1	*Dusicyon culpaeolus*	86·2
Dusicyon gymnocercus	85·3	*Dusicyon microtis*	85·6
Dusicyon culpaeolus	85·3	*Canis mesomelas*	84·3

Following Thomas (1914) many authors have separated the zorro from *Dusicyon* and placed it in either the subgenus or genus *Cerdocyon* Hamilton Smith, 1839. Cabrera (1931) distinguished the species from *Dusicyon* at the generic level on the long dark tail, large feet and characters of the molar teeth and mandibular condyle. The present analysis shows that, although the species lies somewhat apart from the main *Dusicyon* group for some characters, for example the somewhat enlarged frontal sinuses and dark pelage, the numerical results provide no evidence that would justify separate generic status.

Ducisyon microtis (Sclater, 1882)

Small-eared zorro

Distribution. Tropical forests of the Amazonian basin in Brazil, Peru, Ecuador and Colombia. From sea level to 1000 m (Hershkovitz, 1957, 1961). Classified as rare by the *Red data book* (Goodwin & Holloway, 1972).

Description. Larger than the common zorro with a large head, very short, rounded ears, short legs and a long bushy tail. Distinctive, dark, grizzled brown pelage with dark underparts except in the pelvic region where the hair is lighter in colour. The behaviour of this species in captivity has been described by Hershkovitz (1961).

Temporal ridges strongly developed forming a raised, narrow, slightly lyriform sagittal area (as in *Dusicyon australis*). Frontal sinuses quite large as in *Dusicyon thous*, and nasal bones slightly swollen in the facial region. Canines long and 'fox-like'. Cheek-teeth robust.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon thous	86·1	*Canis adustus*	90·4
Canis adustus	84·4	*Dusicyon gymnocercus*	89·7
Dusicyon fulvipes	84·3	*Canis mesomelas*	87·9
Dusicyon gymnocercus	82·9	*Dusicyon culpaeolus*	87·8
Dusicyon sechurae	82·9	*Dusicyon sechurae*	86·6

As with most other members of the South American Canidae there has been a fair amount of vacillation in the classification of the small-eared zorro. Thomas (1914) placed it with the common zorro in the genus *Cerdocyon* Hamilton Smith, 1839. Osgood (1934), on the other hand, believed it to be a true *Dusicyon* within the subgenus *Dusicyon*, whilst he placed only *D. thous* in the subgenus *Cerdocyon*. Cabrera (1940 : 14) considered the small-eared zorro to be quite distinct from *Dusicyon* and he placed it in a new genus *Atelocynus* Cabrera, 1940. Simpson (1945 : 109) noted the new genus but did not use it in his classification. Hershkovitz (1961), however, fully supported Cabrera and believed that the new genus was valid. His reasons were based on the combination of characters that appear to distinguish the small-eared zorro from the rest of the *Dusicyon* species; these being the distinctive pelage, large size, small ears, large heavy teeth and development of the mandibular condyle as in *D. thous*. These characters were observed by Osgood who, nevertheless, retained the species within the genus *Dusicyon*.

The results of this analysis show that *Dusicyon microtis* is phenetically fairly close to *D. thous* and that it lies on the periphery of the main *Dusicyon* group. It could only be argued that it should be given separate generic status if this was also done for *D. australis*. Hershkovitz (1972 : 390) believes that *D. microtis* is a specialized canid adapted to living in tropical rain forest areas.

Genus ***CHRYSOCYON*** Hamilton Smith, 1839

One species.

Chrysocyon brachyurus (Illiger, 1811)

Maned wolf

DISTRIBUTION. Tall grasslands and the outskirts of forests in eastern and southern Brazil, Paraguay, eastern Bolivia and northern Argentina (Cabrera, 1958; Hershkovitz, 1972 : 390). Classified as vulnerable by the *Red data book* (Goodwin & Holloway, 1972).

DESCRIPTION. The largest of the South American canids with a very striking appearance, 'like a fox on stilts'. Shy and solitary, feeding on small prey and some vegetable matter. It is believed that it never digs, and indeed this might be difficult with its long legs. The pelage is distinctive and different from that of any other canid. The hair is long and reddish in colour over the whole body. Muzzle and chin dark, anterior part of throat white and inside of ears white. Feet black from the hocks, which are elongated, downwards. White tuft to rather short bushy tail. The hair along the nape of the neck and back is longer than the rest and dark coloured. Ears large and erect. Flower (1879) recorded that the caecum of a specimen that died in the Zoological Gardens was quite straight.

Skull large and elongated. Frontal bones flat. Temporal ridges close and fused into a well-developed interparietal crest. Palatine bones extend slightly further back than the posterior edge of M^2. Auditory bullae relatively very small. Teeth simple, widely spaced and 'fox-like'. Premolars simple and high-crowned. P^4 short.

Systematic position. Percentage similarity to 'near neighbours' :

All characters		Skull and teeth only	
Canis simensis	79·9	*Canis simensis*	88·7
Dusicyon gymnocercus	74·7	*Canis adustus*	88·7
Dusicyon culpaeolus	74·5	*Dusicyon culpaeolus*	84·3
Dusicyon inca	73·4	*Dusicyon gymnocercus*	83·6
Dusicyon microtis	73·4	*Canis lupus*	82·8

C. brachyurus clearly stands apart on its own. It is not a fox, as is often maintained ; neither does it lie close to the *Canis* group, for although the 'near neighbours' tables do show a fairly high level of similarity with *Canis simensis* and *Canis adustus* these are the two species of *Canis* that are closest to the *Dusicyon* group. A rather low level of similarity with the genus *Dusicyon* is therefore probably the best interpretation of the affinities of the maned wolf and its position on the two-dimensional plots supports this view.

Genus ***SPEOTHOS*** Lund, 1839

One species.

Speothos venaticus (Lund, 1842)

Bush dog

Distribution. Common throughout tropical rainforests and savannah areas in the Brazilian subregion of South America. Also found in one locality in southeastern Panama where Hershkovitz (1972 : 359) suggests that it may have been introduced by man (Cabrera, 1958).

Description. Small, rather 'otter-like' with short legs and tail. Head heavy with a wide muzzle and small ears. Head and neck ochreous fawn or tawny merging into dark brown or black along the back and tail. Chin and underparts as dark as the back. There may be a light patch behind the chin on the throat. Skin of body yellow or tan in colour. The caecum is said to be straight as in *Chrysocyon brachyurus* (Flower, 1880 : 73). The brain has relatively high and massive frontal lobes (reflected in the swollen frontal lobes of the skull) and a relatively untwisted cerebellar vermis (Radinsky, 1973). A social carnivore that hunts in packs of up to ten animals and swims well.

As observed by Huxley (1880), the occiput is unique amongst canids in being drawn out into a short tube (unfortunately this character was missed and has not been taken into account in the numerical analysis). Facial region short with swollen frontal bones producing a slightly convex skull profile. Dentition reduced with M^2 nearly always missing and M_3 always absent, as in *Cuon alpinus*. Canine teeth 'dog-like', that is short and robust. Upper premolars 1–3 unusually thick in cross-section and with no posterior secondary cusps. The talonid or heel of the lower carnassial (M_1) has only one cusp as in *C. alpinus* and *Lycaon pictus* (Table 5). Symphysis of the mandible very long and strongly ankylosed.

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Cuon alpinus	73·5	*Cuon alpinus*	87·0
Dusicyon microtis	68·2	*Nyctereutes procyonoides*	74·1
Lycaon pictus	67·9	*Lycaon pictus*	73·7
Dusicyon australis	67·8	*Dusicyon australis*	72·6
Bloodhound	67·5	Dingo	72·3

Speothos venaticus, *L. pictus* and *C. alpinus* have been placed in the subfamily Simocyoninae by Simpson (1945 : 109, 223) on palaeontological evidence. According to Matthew (1930 : 128) there were two branches of primitive canids during the Miocene. One led to the present-day true canids (subfamily Caninae) whilst the second (the Simocyoninae), which was equally widespread and abundant, later became extinct except for these three representatives. The only diagnostic character that distinguishes the two groups is the development of the talonid of the lower carnassial as a single cusp or ridge in the Simocyoninae. In all other canids the talonid has two cusps and was described by Matthew as 'basined'.

One of the objects of the present work was to test the validity of this grouping on phenetic grounds. While it does appear that the three species are closer to each other than to any other groups on the basis of cranial and dental characters, the overall similarities are very low and it seems best to refrain from emphasizing their very few points of resemblance. Whatever the validity of their common origin they have clearly diverged very greatly and their recognition as isolated monospecific genera seems appropriate.

The bush dog is a highly social animal. Unfortunately there are no detailed studies of the behaviour of *C. alpinus* and the few observations that have been made on *S. venaticus* show that its behaviour patterns are markedly different from those of *L. pictus*. Some habits are shared, however. Both species practise communal sleeping and hunting, neither uses the gape or teeth-baring threats and neither has very highly developed tail-wagging behaviour (Kleiman, 1967).

The behaviour of the bush dog is clearly interrelated with its body-shape and pelage characters. The ventral surface is seldom exposed because the animal has short legs and it therefore has no need for a colour contrasting with the back. The short legs may also be related to the lordosis-like posture held by the female during courtship. The female is said to lower her front legs and raise her hindquarters and tail, as cats do (Kleiman, 1967 : 368). Similarly the lack of facial markings is probably related to the exaggerated submissive grin which exposes the molar teeth rather than a paler cheek region as in the other social canids.

Kleiman maintained (1967 : 371) that *S. venaticus* and *L. pictus* cannot be allied on their behaviour patterns. It would certainly be remarkable if they could be, as the bush dog is highly specialized for hunting in the tropical rainforests of Brazil and the Cape hunting dog (*L. pictus*) for following the migrating herds of large mammals in the African savannah.

Genus ***CUON*** Hodgson, 1838

One species.

Cuon alpinus (Pallas, 1811)

Dhole, red dog, Indian wild dog

Distribution. Montane forest areas of the Indian peninsula, Malaysia, Java, Sumatra, Burma and northwards into Korea, China and eastern U.S.S.R. Not found in Ceylon (Ellerman & Morrison-Scott, 1966). Formerly fairly common but now the distribution of the dhole is much reduced and it is rare. Classified as a vulnerable species by the *Red data book* (Goodwin & Holloway, 1972).

Description. A fairly large 'dog-like' canid with rounded ears and a long, moderately bushy tail. The legs are rather short, the pelage an evenly tawny or dark red colour with slightly darker tail and lighter underparts. The winter coat may be yellowish-grey in cold regions. A social carnivore that lives and hunts in packs.

As observed by Huxley (1880 : 276), there is a notable similarity between the skulls of *Cuon alpinus* and *Lycaon pictus*. In both species the facial region is short and wide, although more so in *Lycaon* than in *Cuon*, and the frontal and maxillary bones are swollen so that the skulls have a convex profile (as in *Speothos venaticus*). The palatine foramina are long in both species and the nasal bones widen at the point where they meet the suture between the frontal and maxillary bones (the nasals are often described as having a sigmoid shape). In both species the dentition is 'dog-like' and strongly developed except that M^2 is reduced in size and, in *Cuon*, M_3 is absent. Secondary posterior cusps are present on P^2, P^3, and on the lower premolars in both species. The talonid of the lower carnassial (M_1) has only one cusp in *Cuon* as it has in *Speothos* and *Lycaon*. This character was first observed by Major in 1872 (1900 : 834).

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon australis	79·2	*Speothos venaticus*	87·0
Dusicyon gymnocercus	78·2	*Lycaon pictus*	80·9
Canis latrans	77·9	Dingo	78·6
Dingo	77·3	*Dusicyon australis*	76·0
Canis aureus	77·0	*Canis lupus*	75·2

Pocock (1941 : 146) was not impressed with the assumed similarities between *C. alpinus* and *L. pictus* that had been described by previous authors and he was even less impressed by the similarities between *Cuon* and *Speothos*. Our numerical results, however, show that there are certain phenetic resemblances in the skulls and teeth of the three genera but the pelage and postcranial characters are widely different and although all three are social species without highly developed facial expressions it is not known whether there are any inherent behaviour patterns that link the three genera. Kleiman's comparative study (1967) did not include *Cuon*, and *Lycaon* is the only one of the three on which serious ethological studies have been carried out (van Lawick–Goodall, 1970 ; Kühme, 1965a, b).

Although the dhole may resemble the dingo and the Indian pariah dog in colouring and superficial appearance, the skull and teeth are so distinctive that it is most unlikely that this species has contributed to the ancestry of the domestic dog.

Genus ***LYCAON*** Brookes, 1827

One species.

Lycaon pictus (Temminck, 1820)

Hunting dog

DISTRIBUTION. Formerly widespread throughout the African savannah south of the Sahara wherever game was abundant, up to 2700 m. Now becoming increasingly restricted to game reserves (Allen, 1939 ; Ellerman *et al.*, 1953). Classified as a vulnerable species by the *Red data book* (Goodwin & Holloway, 1972).

DESCRIPTION. A large canid with long legs and a heavy, rather 'hyaena-like' head. Ears large, rounded and nearly naked. Body hair may be scant. Mottled pelage which is variable in pattern and colouring. The irregular spots may be black, brown, grey or white, on a basic colour of yellowish-grey or black. The muzzle is dark and may have a dark stripe leading along the side of the head. Tail moderately bushy with a white tip. This species is the only member of the Canidae in which the first digit is absent or vestigial in the fore feet as well as the hind feet. Highly social but has never been domesticated.

Short wide facial region with swollen frontal maxillary bones that give a convex shape to the skull profile, as in *Cuon alpinus*. The anterior palatine foramina are large and the nasal bones are wide. Frontal sinuses well developed. Interparietal crest may be pronounced. Dentition complete with strong, 'dog-like' canines and carnassials. Posterior secondary cusps are present on P^2, P^3 and on the lower premolars. The talonid of the lower carnassial, M_1, has only one cusp, as in *Speothos* and *Cuon.*

SYSTEMATIC POSITION. Percentage similarity to 'near neighbours':

All characters		Skull and teeth only	
Dusicyon australis	71·0	Dingo	81·8
Cuon alpinus	69·7	*Cuon alpinus*	80·9
Bloodhound	68·8	*Canis lupus*	79·4
Dingo	67·9	*Canis aureus*	77·6
Speothos venaticus	67·9	Bloodhound	77·4

The numerical results show that *Lycaon pictus* is a most aberrant canid and there can be no dispute about its generic status. The phenetic relationships of this species with *Speothos* and *Cuon* have already been discussed in the sections on these genera.

REMARKS. The hunting dog occupies the 'wolf niche' in Africa. The species has evolved a system of ritualized communal feeding whereby a whole pack can be sustained on the hunting efforts of a few individuals (Kühme, 1965a, b). This system is based on the regurgitation of food by the hunters for the juveniles and all members of the pack that have not joined in the killing of prey (usually antelope or gazelle). Many species of canid will regurgitate food for their young but in the hunting dog this habit is extended and has evolved into a basis for highly organized social behaviour. Although it is perhaps the most social of all canids the hunting dog has not evolved the elaborate facial expressions and signals of communication that are now so well known from studies of behaviour in the wolf. Fox (1970) suggested that the reasons for this are that the social organization of the hunting dog is based on individual dominant and subordinate relationships, mutual submission and strong group-orientated activities, rather than on a hierarchy of relationships as occurs within the wolf pack. He further suggests that communication by facial expression is important to groups of wolves that frequently undergo separation and congregation, whereas the hunting dog packs remain together as cohesive units for longer periods. Perhaps the strikingly individual markings of the hunting dog also assist in communication and identification of conspecifics.

ACKNOWLEDGEMENTS

Computer time for this project was kindly supplied by Rothamsted Experimental Station and we are most grateful to Miss Linda Jackson for her help in running the programs. Our thanks are also due to Miss Jenny Paul who assembled much of the data during tenure of a vacation studentship at the British Museum (Natural History).

APPENDIX I: DATA MATRICES

TABLE 4

Characters of the skull

	1	2	3	4	5	6	7	8	9	10	11	12	13
Canis lupus	226	65	33	51	88	57	14	3	3	2	1	2	0
Dingo	180	64	32	50	80	57	14	2	3	2	1	2	0
Bloodhound	221	63	35	56	83	49	12	3	3	2	1	2	0
Canis latrans	180	59	28	48	93	52	14	2	3	2	1	2	0
C. aureus	160	65	34	52	85	57	16	2	3	2	1	2	0
C. mesomelas	144	64	32	51	79	59	16	2	3	2	1	1	0
C. adustus	149	60	30	50	89	51	14	2	3	2	1	1	0
C. simensis	183	52	25	49	94	53	13	1	2	2	1	1	0
Vulpes vulpes	130	55	29	54	88	54	15	1	2	2	1	0	0
V. corsac	112	58	31	53	81	59	17	1	1	2	0	0	0
V. ferrilata	145	49	24	51	115	57	15	1	1	2	0	0	0
V. bengalensis	112	58	29	50	89	56	18	1	1	2	1	0	0
V. cana	90	58	26	45	87	56	19	0	0	0	0	0	0
V. rueppelli	102	57	27	47	94	55	20	1	1	2	1	0	0
V. pallida	98	59	30	51	83	55	18	1	0	1	1	0	0
V. zerda	82	60	29	49	89	54	26	0	0	0	0	0	0
V. chama	111	60	30	50	83	55	18	1	1	2	1	0	0
V. velox	114	56	26	46	89	54	17	1	1	1	1	0	0
V. cinereoargenteus	119	55	28	51	85	56	16	2	0	2	2	0	1
Alopex lagopus	124	62	35	56	81	56	16	1	2	2	0	0	0
Otocyon megalotis	114	54	32	60	81	54	17	2	0	1	2	0	2
Nyctereutes procyonoides	110	59	35	59	83	57	17	1	2	2	2	2	1
Dusicyon australis	157	64	34	53	75		15	2	1	2	1	2	0
D. culpaeus	165	53	24	45	124	55	14	2	3	2	1	1	0
D. culpaeolus	139	57	29	50	91	56	15	1	2	2	1	1	0
D. gymnocercus	139	55	28	51	91	53	16	1	1	2	1	1	0
D. inca	147	55	28	51	98	56	13	1	3	2	2	1	0
D. griseus	120	55	27	48	92	51	15	0	1	1	0	1	0
D. fulvipes	115	59	30	50	93	54	16	0	0	1	1	1	0
D. sechurae	117	58	32	54	82	57	15	1	1	2	1	2	0
D. vetulus	104	65	36	55	74	59	19	1	1	2	1	2	0
D. thous	126	62	31	50	90	53	15	0	1	1	1	1	1
D. microtis	149	60	32	54	94	58	15	2	1	2	1	1	1
Chrysocyon brachyurus	213	54	28	52	95	56	12	3	3	2	1	1	0
Speothos venaticus	124	67	41	62	75	58	15	1	2	2	2	2	0
Cuon alpinus	178	70	40	57	72	61	15	1	3	2	1	2	0
Lycaon pictus	188	76	47	62	61	68	15	2	3	2	0	2	0

TABLE 4 cont.

Key to characters
1. Condylobasal length
2. Palate – greatest width as % of length of palate (a : b).
3. Rostrum – width as % of length of palate (c : b).
4. Rostrum – width as % of width of palate (c : a).
5. Premaxillae – anterior palatine length as % of width of rostrum (d : c).
6. Zygomatic width as % of condylobasal length (e : 1).
7. Bullae – maximum length as % of condylobasal length (f : 1).
8. Temporal ridges – size : 0 = absent ; 3 = highly developed.
9. Temporal ridges – proximity : 0 = wide apart ; 3 = fused.
10. Interparietal crest : 0 = absent ; 2 = well developed.
11. Parietal bones – rugosity : 0 = smooth ; 2 = distinctly rugose.
12. Post-orbital processes – convexity : 0 = concave ; 1 = flat ; 2 = strongly convex.
13. Mandible – size of subangular lobe : 0–2.

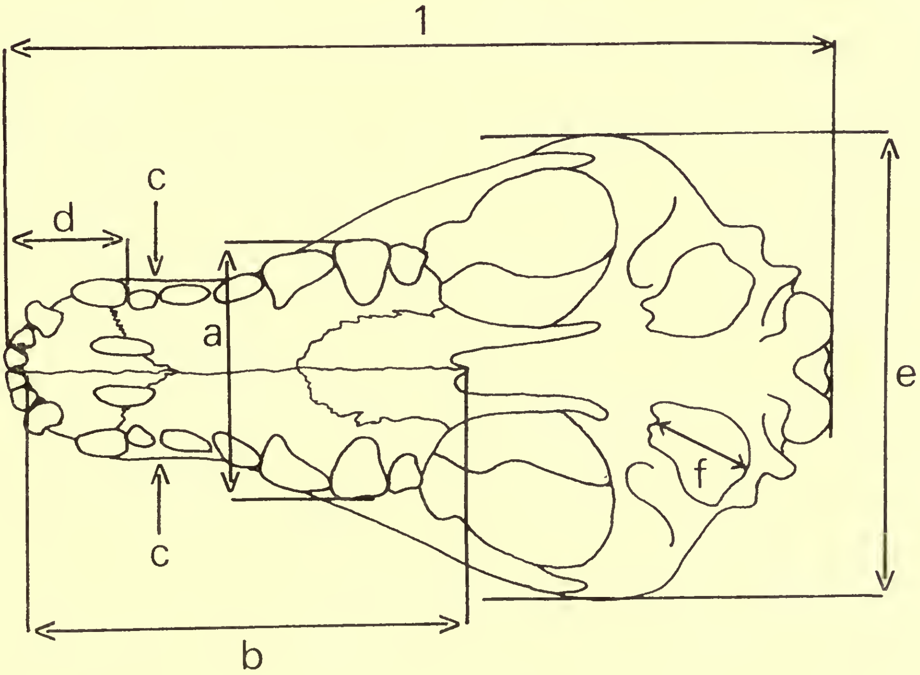


TABLE 5

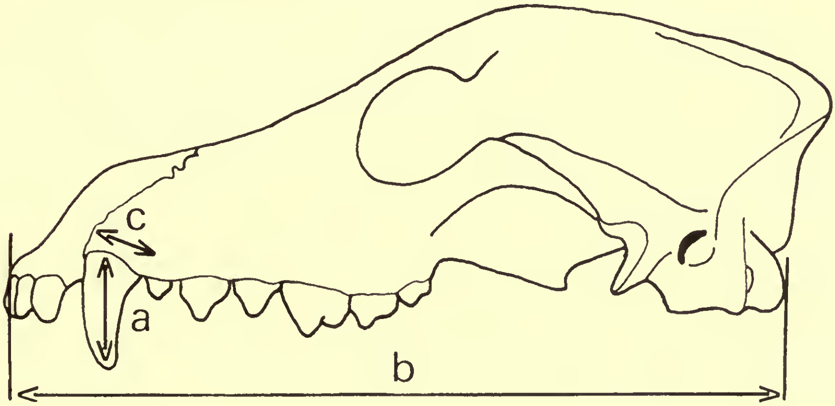
Characters of the teeth

	upper								lower			deciduous	
	1	2	3	4	5	6	7	8	9	10	11	12	13
Canis lupus	11	50	2	11	0	1	6	0	1	1	0	0	1
Dingo	11	48	2	11	0	1	6	0	1	1	0	0	1
Bloodhound	11	54	2	9	0	1	6	0	1	1	0	0	1
Canis latrans	12	42	2	11	0	1	7	0	1	1	0		
C. aureus	11	50	2	10	0	1	6	0	1	1	0	1	1
C. mesomelas	11	41	1	11	0	1	7	0	1	1	0	1	1
C. adustus	11	40	1	9	0	1	7	0	1	1	0	1	1
C. simensis	12	39	1	9	0	1	6	0	1	1	0	1	1
Vulpes vulpes	12	37	1	10	0	1	6	0	1	1	0	1	0
V. corsac	12	41	1	10	0	1	6	0	1	1	0		
V. ferrilata	14	35	1	9	0	1	6	0	1	1	0	0	1
V. bengalensis	12	36	1	9	0	1	8	0	1	1	0	1	0
V. cana	9	38	0	11	0	1	7	0	1	1	0		
V. rueppelli	9	47	1	10	0	1	7	0	1	1	0	1	0
V. pallida	10	41	1	8	0	1	8	0	1	1	0		
V. zerda	10	35	1	9	0	1	8	0	1	1	0	1	0
V. chama	10	37	1	9	0	1	7	0	1	1	0		
V. velox	11	37	1	10	0	1	6	0	1	1	0		
V. cinereoargenteus	8	51	1	8	0	1	7	0	1	1	0	1	0
Alopex lagopus	11	49	2	10	0	1	6	0	1	1	0	1	0
Otocyon megalotis	8	47	0	5	1	1	6	1	1	1	1	1	0
Nyctereutes procyonoides	10	46	1	9	0	1	6	0	1	1	0		
Dusicyon australis	12	43	1	11	0	1	6	0	1	1	0		
D. culpaeus	13	36	1	10	0	1	7	0	1	1	0	1	0
D. culpaeolus	11	41	2	10	0	1	7	0	1	1	0		
D. gymnocercus	11	40	1	10	0	1	7	0	1	1	0		
D. inca	13	39	2	11	0	1	7	0	1	1	0		
D. griseus	11	37	1	10	0	1	7	0	1	1	0	1	0
D. fulvipes	11	35	1	10	0	1	7	0	1	1	0		
D. sechurae	12	38	1	9	0	1	7	0	1	1	0	1	1
D. vetulus	12	37	0	7	0	1	8	0	1	1	0		
D. thous	9	46	1	10	0	1	8	0	1	1	0	1	1
D. microtis	13	39	1	9	0	1	7	0	1	1	0		
Chrysocyon brachyurus	11	44	0	8	0	1	6	0	1	1	0		
Speothos venaticus	11	50	2	10	0	0		0	0	0	0	0	0
Cuon alpinus	10	53	2	11	0	1	4	0	0	0	0	0	0
Lycaon pictus	12	50	2	11	0	1	5	0	0	1	0	0	1

TABLE 5 cont.

Key to characters

1. C^1 – height as % of condylobasal length (a : b).
2. C^1 – alveolar length as % of height (c : a).
3. P^3 – posterior cusps present : 0–2.
4. P^4 (carnassial) – length as % of condylobasal length (d : b).
5. P^4 – shape : 0 = carnassial ; 1 = molariform.
6. M^2 present : 0–1.
7. M^2 – greatest width as % of condylobasal length (e : b).
8. M^3 present : 0–1.
9. M_1 (carnassial) – two cusps on heel : 0–1.
10. M_3 present : 0–1.
11. M_4 present : 0–1.
12. DP^3 – protocone developed as a cusp : 0–1.
13. DP^4 – posterior border concave, so that metacone appears as a separate lobe : 0–1.



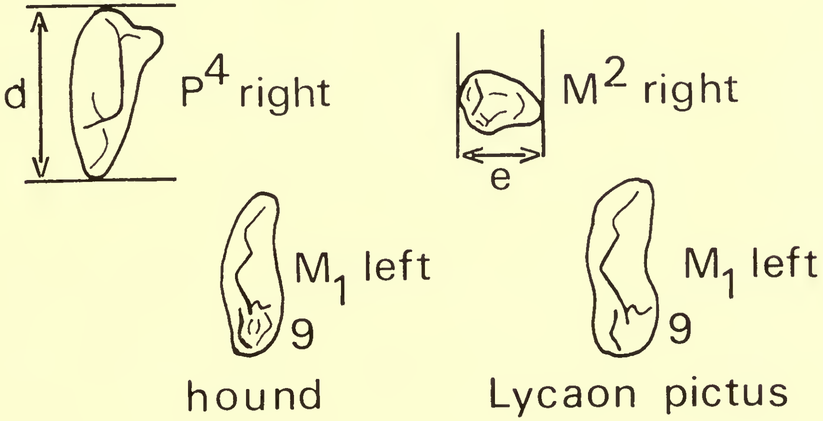

d
P4 right
M2 right
e
M1 left
9
M1 left
9
hound
Lycaon pictus

TABLE 6

Pelage of head and body

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Canis lupus	2	0	0	0	0	0	0	0	1	0	2	0	2	1	1	2	0
Dingo	3	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0
Bloodhound	2	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0
Canis latrans	1	1	0	0	0	0	0	0	1	0	1	0	2	1	1	2	0
C. aureus	1	2	0	0	0	0	2	0	1	0	1	0	2	1	1	2	0
C. mesomelas	1	1	0	0	0	0	2	0	1	0	3	0	2	1	1	2	0
C. adustus	1	1	0	0	0	0	2	0	0	1	0	0	2	1	1	2	0
C. simensis	0	3	0	0	0	0	1	0	1	0	0	0	1	1	1	1	0
Vulpes vulpes	1	3	0	0	1	0	2	0	0	0	0	0	1	2	1	2	0
V. corsac	1	1	0	0	1	0	2	0	0	0	0	0	1	1	1	1	0
V. ferrilata	1	1	0	0	0	0	2	0	0	0	0	0	1	1	1	2	0
V. bengalensis	1	1	0	0	1	0	2	0	0	0	0	0	1	1	1	2	0
V. cana	1	0	0	0	1	0	2	0	0	0	1	0	0	1	1	2	0
V. rueppelli	1	1	0	0	1	0	2	0	0	0	0	0	1	1	1	2	0
V. pallida	1	1	0	0	0	0	2	0	0	0	0	0	1	1	0	1	0
V. zerda	0	1	0	0	0	0	2	0	0	0	0	0	0	1	1	2	0
V. chama	1	1	0	0	0	0	2	0	0	0	0	0	1	2	1	2	0
V. velox	0	1	0	0	1	0	2	0	0	0	0	0	1	1	1	2	0
V. cinereoargenteus	1	1	0	0	1	0	2	0	0	0	0	0	1	1	1	1	0
Alopex lagopus	2	0	0	0	0	0	1	0	0	0	0	0	0	2	0	2	1
Otocyon megalotis	1	1	0	1	0	0	2	0	0	0	0	0	1	2	1	2	0
Nyctereutes procyonoides	1	2	0	0	0	1	1	0	0	0	0	0	2	2	1	2	0
Dusicyon australis	1	2	0	0	0	0		0	0	0	0	0	1	1	1	2	0
D. culpaeus	1	1	0	0	0	0	2	0	0	0	1	0	1	1	1	1	0
D. culpaeolus	1	1	0	0	0	0	2	0	0	0	1	0	1	1	1	2	0
D. gymnocercus	1	1	0	0	0	0	2	0	0	0	0	0	1	1	1	1	0
D. inca	1	1	0	0	0	0	2	0	0	0	0	0	1	1	1	1	0
D. griseus	1	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0
D. fulvipes	2	1	0	0	0	0	2	0	0	0	0	0	1	1	1	1	0
D. sechurae	1	0	0	0	0	0	2	0	0	0	0	0	1	1	1	1	0
D. vetulus	1	1	0	0	0	0	2	0	0	0	0	0	1	1	1	1	0
D. thous	2	1	0	0	0	0	1	0	1	0	1	0	2	1	1	1	0
D. microtis	3	1	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0
Chrysocyon brachyurus	1	3	0	1	0	0	1	0	2	0	2	0	1	2	0	1	0
Speothos venaticus	2	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Cuon alpinus	0	3	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0
Lycaon pictus	2	2	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0

Table 6 cont.

Key to characters

1. Overall colour – intensity of black pigment: 0 = absent; 1 = grey or banded hairs; 2 = general appearance dark; 3 = very dark.
2. Overall colour – intensity of red pigment: 0 = absent; 1 = present as yellow or red underfur; 2 = general appearance reddish or tan; 3 = extensive red colour.
3. Pelage boldly spotted: 0–1.
4. Muzzle dark: 0–1.
5. Facial mask between nose and eye: 0–1.
6. Facial mask behind and below eye: 0–1.
7. Mystacial vibrissae – length and thickness: 0–2 (Hildebrand, 1952b).
8. Crown – dark median stripe: 0–1.
9. Neck and back with crest or mane: 0–2.
10. Side – dark and light longitudinal bands: 0 = absent; 1 = present.
11. Back – dark longitudinal band: 0 = absent; 1 = narrow stripe; 2 = wide stripe; 3 = saddle.
12. Ventral pelage dark: 0 = paler than rest of body; 1 = dark.
13. Guard hairs – coarseness: 0–2.
14. Dorsal guard hairs – length in relation to body size: 0–2.
15. Dorsal guard hairs banded (agouti): 0–1.
16. Underfur – density: 0–2.
17. Seasonal colour change: 0–1.

TABLE 7

Pelage of extremities ; other external characters

	ears				tail				fore legs			hind legs					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Canis lupus	11	0	0	1	38	2	1	2	0	1	1	0	0	22	0	0	10
Dingo	11	0	0	0	35	0	0	1	0	0	1	0	0	20	1	0	
Bloodhound		0	0	0		0	0	1	0	0	1	0	0		1	0	10
Canis latrans	13	0	0	0	33	2	1	1	0	1	1	0	0	21	0	0	8
Canis aureus	12	0	0	0	35	1		2	0	1	1	0	0	17	0	0	
C. mesomelas	15	0	0	0	44	2		2	0	0	1	0	0	22	0	0	
C. adustus	12	0	0	0	52	1		2	0	1	1	0	0	22	0	0	
C. simensis	11	0	0	0	25	1	0	2	0	0		0	0	20		0	
Vulpes vulpes	16	0	1		59	2	0	0	0	1	1	0	0	25	0	0	8
V. corsac	9	0	0	0	35	2	1	2	0	0		0	0			0	
V. ferrilata	8	0	0	0	43	1	1	1	0	0		0	0	19		0	
V. bengalensis	15	0	0	0	58	2	1	2	0	0		0	0	24		0	6
V. cana	18	0	1	0	71	2	0	1	0	0		0	1	21		0	
V. rueppelli	21	0	0	0	76	2	1	0	0	0		0	0	25		0	
V. pallida	17	0	0	0	60	1	1	2	0	0	1	0	0	24	0	0	
V. zerda	25	0	0	0	56	1	1	2	0	0	1	0	0	25	0	0	
V. chama	20	0	0	0	69	2	1	2	0	0		0	0	26		0	
V. velox	17	0	0	0	35	2	1	2	0	0		0	0	26		0	
V. cinereo-argenteus	14	0	0	0	69	1	2	2	0	0	1	0	0	24	0	0	6
Alopex lagopus	9	1	0	0	59	2	0	1	0	0	1	0	0	24	0	0	12
Otocyon megalotis	23	0	1	0	55	2	0	2	1		1	1	0	25	0	0	
Nyctereutes procyonoides	9	1	0	1	37	1	0	1	1		1	1		20	0	0	
Dusicyon australis	7	0	0	0	29	1	1	0	0	0		0	0	19		0	
D. culpaeus	13	0	0	0	58	2	1	2	0	0	1	0	0	23	0	0	
D. culpaeolus		0	0	0		2	1	2	0	0		0	0			0	
D. gymnocercus	13	0	0	0	53	2	1	2	0	0		0	0	22		0	
D. inca	15	0	0	0	50	1	1	2	0	0		0		22		0	
D. griseus	15	0	0	0	62	2	1	2	0	0	1	0		24	0	0	
D. fulvipes	14	0	0	0	41	1	1	2	0	0		0		22		0	
D. sechurae	14	0	0	0	57	1	1	2	0	0		0	0	22		0	
D. vetulus	12	0	0	0	54	2	1	2	0	0		0	0	21		0	
D. thous	10	0	0	0	45	1	2	2	0	0	1	0	1	21	0	0	
D. microtis	10	0	0	0	43	1	2	2	1			1		19		0	
Chrysocyon brachyurus	14	0	0	0	22	2	0	0	1		1	1		22	0	0	
Speothos venaticus	8	1	0	0	24	0	0	1	1		1	1		18	0	1	8
Cuon alpinus	12	0	0	0	41	1	0	2	0	0	1	0	0	24	0	0	14
Lycaon pictus	14	1	0	1	36	1	0	0	0	0	0	0	0	24	0	2	10

TABLE 7 cont.

Key to characters

1. Ears – length as % of length of head and body (from skin labels and collector's notes, therefore only approximate).
2. Ears rounded : 0–1.
3. Ears dark : 0–1.
4. Ears – dark rim : 0–1.
5. Tail – length as % of length of head and body (as for 1).
6. Tail – bushiness : 0–2.
7. Tail – dark patch on dorsal surface (see Hildebrand, 1952b) : 0 = absent ; 2 = long.
8. Tail – tip dark : 0 = white ; 1 = same as rest of tail ; 2 = black.
9. Fore legs entirely dark : 0–1.
10. Fore legs with black line on front : 0–1.
11. Fore feet – claws on digit 1 : 0–1.
12. Hind legs dark : 0–1.
13. Hind feet – dark plantar surface : 0–1.
14. Hind feet – length as % of length of head and body (as for 1).
15. Hind feet – claw on digit 1 : 0–1.
16. Skin – darkly pigmented : 0–2.
17. Mammae – total number (from Hildebrand, 1952b).

TABLE 8

Body proportions ; post-cranial skeleton ; internal anatomy

										baculum				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Canis lupus	71	79	39	1	1	73	97	8	42	53	0	0	0	
Dingo	67	73	43	1	1	70	102	6	40					
Bloodhound	69	77	43	1	1		99	8	39					
Canis latrans	70	78	41	1	0				45		0	0	0	
C. aureus	62	73	44	1	1	67	97	7	44	34	0	0	0	2
C. mesomelas	66	75	46	0	1	67	100	6	43	35	0	0	0	
C. adustus	71	77	43	0	1	56	93	7	46					
C. simensis														
Vulpes vulpes	70	81	38	0	0	71	96	7	41	36	1	0	0	2
V. corsac														
V. ferrilata														
V. bengalensis														
V. cana														
V. rueppelli														2
V. pallida	63	78	40	1	0	76	85	8	52	41	0	0	0	
V. zerda	68	83	39	2	0	75	80	8	53		0	0	0	2
V. chama														2
V. velox	66	78	39											
V. cinereoargenteus	59	73	39	0	0	63	96	8	50	43	0	0	0	
Alopex lagopus	70	79	34	1	0	76	89	7	49	49	0	0	0	2
Otocyon megalotis	70	82	42	1	0	77	94	7	46	58	1	0	0	2
Nyctereutes procyonoides	59	69	42	2	0	53	95	8	43	50	0	0	0	1
Dusicyon australis														2
D. culpaeus	65	76	38	1	0	63	93	7		41	0	0	0	2
D. culpaeolus														
D. gymnocercus														2
D. inca														
D. griseus	64	75	38	1	0		95	6	43	43	0	0	0	
D. fulvipes										43	0	0	0	
D. sechurae														
D. vetulus	57	67	40							47	0	0	0	
D. thous	57	67	41	1	0	54			48	43	0	0	0	1
D. microtis														
Chrysocyon brachyurus	92	103	47	2	0	60	95	6	49	34	0	0	1	0
Speothos venaticus	52	58	37	0	0	71	108	8	37					0
Cuon alpinus	60	70	35	2	0	60	104	8	42		0	0	0	2
Lycaon pictus	68	74	38	0	1	68	97	7	41	52	1	1	0	2

TABLE 8 cont.

Key to characters

1. Fore legs – length as % of length of body spine (cervical to lumbar vertebrae) (from Hildebrand, 1952a : fig. 6).
2. Hind legs – length as % of length of body spine (as above).
3. Neck – length of cervical vertebrae as % of combined length of thoracic and lumbar vertebrae (from Hildebrand, 1952a : fig. 14).
4. Scapula – shape of *teres major* muscle scar on posterior angle : 0 = on posterior border only, with plane at right angles to lateral face ; 1 = intermediate ; 2 = whole scar on lateral face.
5. Scapula – extent of scar of *serratus magnus* muscle on medial side : 0–1.
6. Pelvis – width as % of length (a : b).
7. Femur – length as % of length of tibia (c : d).
8. Femur – minimum width of shaft as % of length (f : c).
9. Third metatarsal – length as % of length of femur (e : c).
10. Baculum – length as % of condylobasal length.
11. Baculum – anterior end bifurcate : 0–1.
12. Baculum – well-defined protuberance on dorsal keel : 0–1 (see Hildebrand, 1954, fig. 15).
13. Baculum – well-defined dorsal protuberance but no keel : 0–1 (as for 12).
14. Caecum – shape : 0 = straight ; 1 = nearly straight ; 2 = convoluted (from Flower, 1879, 1880 ; Garrod, 1873, 1878).

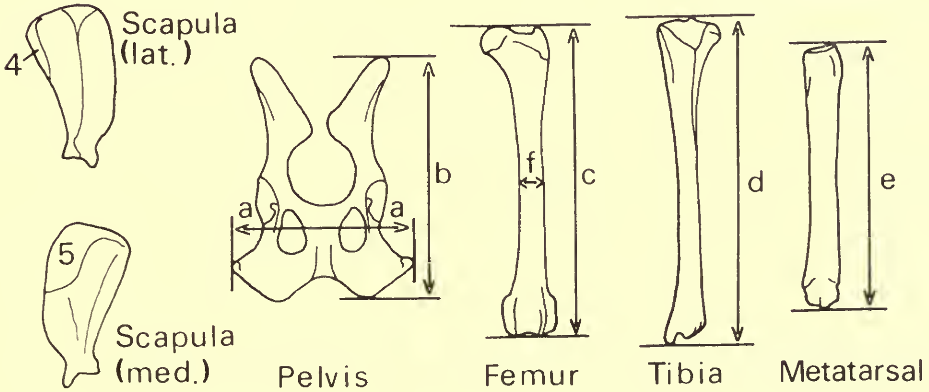


TABLE 9

Behaviour

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Canis lupus	2	2	3	0	0	0	2	0	0	1	0	0	1	1	2	1
Dingo	1	0	2	0	0	0	1	0	0	1	0	0	0	1	2	1
Bloodhound							1	1	0	1	0	0	1		2	
Canis latrans	1	2	1	0	0	0	2	0	0	1	0	0	1	1	2	1
C. aureus		0		0	0	0	2	0	0	1	0	0	1	1	2	1
C. mesomelas	0	0	1	0	0	0		0	0	1	0	0	1		2	1
C. adustus	0	0	1	0	0	0		0	0	1	0	0	1		2	1
C. simensis																
Vulpes vulpes	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
V. corsac																1
V. ferrilata																
V. bengalensis																1
V. cana																
V. rueppelli																
V. pallida																
V. zerda																1
V. chama																
V. velox																1
V. cinereoargenteus																
Alopex lagopus	0	1	1	0	0	0		0	0	1	0		0	0	1	1
Otocyon megalotis	0	1	2	0	1	1		0	0	1	0		3	0	2	1
Nyctereutes procyonoides		0	2	0	1	1		0	0	1	0		3	0	0	1
Dusicyon australis																
D. culpaeus																1
D. culpaeolus																
D. gymnocercus		1	1	0	0	0		0	0	1	0		1	0	2	
D. inca																
D. griseus																
D. fulvipes																
D. sechurae																
D. vetulus																
D. thous		0														
D. microtis																
Chrysocyon brachyurus	0	0	0	0	0	0	0	0	0	1	0	1	2	0	1	0
Speothos venaticus	2	2	3	0	0	1	2	1	1	1	1	0		0	2	
Cuon alpinus	2	2	2	0	0	0		0	0	1	0			0	2	1
Lycaon pictus	2	2	3	1	0	1		1		0	0			0	2	1

TABLE 9 cont.

Key to characters (from Kleiman, 1966, 1967)

1. Diet – size of prey relative to body size : 0–2.
2. Diet – proportion of meat : 0 = varied – insects, vegetable, small vertebrates, carrion ; 1 = varied – insects and small vertebrates ; 2 = mainly vertebrates.
3. Hunt socially : 0 = singly ; 1 = singly or in pairs ; 2 = pairs or family groups ; 3 = packs.
4. Ritual feeding : 0–1.
5. Social grooming : 0 = rare and only between pairs ; 1 = well developed.
6. Communal sleeping : 0–1.
7. Howling : 0 = absent or only as long-distance contact call ; 1 = present but no physical contact ; 2 = close-contact call, social howling in unison.
8. Frequency of oestrus phases for year : 0 = once ; 1 = twice.
9. Female courtship posture : 0 = normal standing position as in domestic dog ; 1 = crouching position (lordosis) as in the cat.
10. Copulatory tie present : 0–1.
11. Urination in a spray : 0–1.
12. Defecation at specific sites : 0–1.
13. Tail posture in dominant animals : 0 = no distinct posture ; 1 = straight and horizontal ; 2 = raised in a J-shape ; 3 = inverted U-shape.
14. Extent of teeth-baring in dominant threat posture : 0–1.
15. Frequency of tail-wagging in submissive posture : 0–2.
16. Regularly occupies an underground den : 0–1.

APPENDIX II: LICE (PHTHIRAPTERA) OF THE CANIDAE

The identification of ectoparasites, particularly lice which are often rigidly host-specific, can sometimes expose interesting relationships between different groups of animals. The following species of lice are listed by Hopkins (1949) as known to parasitise members of the Canidae:

Mallophaga, biting lice

Trichodectes (*Trichodectes*) *canis* de Geer

Canis lupus †
Domestic dog, including dingo * †
Canis latrans †
Canis aureus, one record from a captive host
Dusicyon culpaeus, one record
Dusicyon fulvipes, one record, apparently from a wild host
Dusicyon thous †

Felicola (*Suricatoecus*) *vulpis* Denny

Vulpes vulpes * †
Vulpes cinereoargenteus †

Felicola (*Suricatoecus*) *guinlei* Werneck

Otocyon megalotis *

Felicola (*Suricatoecus*) *fahrenholzi* Werneck

Dusicyon fulvipes * †
Dusicyon sechurae, one record from a museum skin

Heterodoxus spiniger Enderlein

Domestic dog * †
Canis latrans †
Canis aureus †
Canis adustus and *Cuon alpinus* (see Kéler, 1971)

Anoplura, sucking lice

Linognathus setosus von Olfers

Canis lupus, one record, apparently on a wild host
Domestic dog * †
Canis latrans, one record, no details
Canis aureus, one record, apparently on a wild host
Canis mesomelas †
Vulpes vulpes, one record on a captive host
Alopex lagopus †

Linognathus taeniotrichus Werneck

Dusicyon fulvipes, one record on a captive host
Dusicyon thous * †

---

* Nominal host for the species of louse listed.
† Natural occurrence of the species of louse established on this canid.

The genus *Heterodoxus* is particularly interesting for, with the single exception of *Heterodoxus spiniger*, its hosts are confined to Australian marsupials. *H. spiniger* has the domestic dog for its nominal host and has been recorded frequently from the coyote and jackals. Until recently this species of *Heterodoxus* was not known to occur on marsupials but there is now a record (Kéler, 1971) for its presence on the wallaby, *Wallabia agilis*. Before this confirmed report Hopkins (1949) suggested that the species had evolved after transference to the dingo from a marsupial, perhaps shortly after dogs were introduced by man to Australia. This could have been in the early Holocene. The louse would then have spread to domestic dogs and thence to other wild canids as human populations moved about the world. At the present day *H. spiniger* is widespread on canids in many parts of Africa, Australia, America and Asia, but not apparently in Europe, Antarctica nor the northern regions of North America. Now that it is known, however, that *H. spiniger* does occur on a marsupial host it is possible that the transference to the dingo occurred at a later period; on the other hand, its presence on the wallaby could be a secondary transference back to a marsupial host.

The relationship between *H. spiniger* and its canid and marsupial hosts is obviously complicated, but it is possible that further work could throw light on the movements of human populations and the origins of their domestic dogs during the prehistoric period.

Support for the inclusion of the American grey fox (*Urocyon cinereoargenteus*) within the genus *Vulpes*, as proposed in this classification, is given by the louse, *Felicola vulpis*, which has been identified from both the common fox and the grey fox.

It was hoped there might be evidence for louse infestation on the skins of the extinct Falkland Island wolf, *Dusicyon australis*, and that this would lead to information on the relationships of this enigmatic canid. An examination (by Mr C. Moreby, British Museum (Natural History)) of the two skins that are in the Museum collections failed to produce any signs of lice; as incidentally did the mummified skin of an Ancient Egyptian dog, also in the collections.

REFERENCES

Allen, G. M. 1939. A checklist of African mammals. *Bull. Mus. comp. Zool. Harv.* **83**: 1–763.

Anon. 1950. *Bull. zool. Nomencl.* **4**: 549.

Blanford, W. T. 1888. *The fauna of British India including Ceylon and Burmah. Mammalia.* London.

Bobrinskii, N. A. 1965. Order Carnivora. *In* Bobrinskii, N. A., Kuznetsov, B. A. and Kuzyakin, A. P. [*Key to the Mammals of the USSR*]. Moscow (in Russian).

Bowdich, T. E. 1821. *An analysis of the natural classifications of Mammalia.* Paris: 40.

Brink, F. H. van den. 1973. Distribution and speciation of some carnivores – 2. *Mammal Review*, **3**: 85–95.

Bueler, L. E. 1974. *Wild dogs of the world.* London.

Burmeister, C. H. C. 1854. *Systematische Uebersicht der Thiere Brasiliens.* Berlin.

Cabrera, A. 1931. On some South American canine genera. *J. Mammal.* **12**: 54–67.

CABRERA, A. 1958. Catalogo de los mamiferos de America del sur, I. *Revta Mus. argent. Cienc. nat. Bernardino Rivadavia* (*Cienc. Zool.*), **4** : 1–307.

—— & YEPES, J. 1940. *Mamiferos Sud-Americanos* (*vida, costumbres y descripción*). Buenos Aires : 1–370.

CHIARELLI, A. B. 1975. The chromosomes of the Canidae. *In* Fox (1975) : 40–53.

CLUTTON-BROCK, J. 1969. Carnivore remains from the excavations of the Jericho Tell. *In* Ucko, P. J. & Dimbleby, G. W. (eds), *The domestication and exploitation of plants and animals.* London : 337–345.

—— & CORBET, G. B. 1975. *Vulpes* Frisch, 1775 : proposed conservation under the plenary powers. *Bull. zool. Nomencl.* **32** : 110–112.

CORBETT, L. & NEWSOME, A. 1975. Dingo society and its maintenance : a preliminary analysis. *In* Fox (1975) : 369–379.

CREEL, G. C., THORNTON, W. A. & TRIMBLE, R. E. 1971. Hybridization in the fox genus *Vulpes* in west Texas. *S. West Nat.* **15** : 473–484.

—— —— 1974. Comparative study of a *Vulpes fulva* – *Vulpes macrotis* hybrid fox karyotype. *S. West. Nat.* **18** : 465–468.

CRISLER, L. 1959. *Arctic wild.* London.

DARWIN, C. 1860. *Journal of researches into the natural history and geology of the countries visited during the voyage of HMS Beagle round the world.* London : 280.

—— & WATERHOUSE, G. R. 1840. *The zoology of the voyage of HMS Beagle. Mammalia.* London.

ELLERMAN, J. R. & MORRISON-SCOTT, T. C. S. 1966. *Checklist of palaearctic and Indian mammals 1758 to 1946*, 2nd ed. London.

—— —— & HAYMAN, R. W. 1953. *Southern African Mammals 1758–1951 : a reclassification.* London.

FLEMING, J. 1822. *The philosophy of zoology, or a general view of the structure, functions, and classification of animals.* Edinburgh & London, vol. 2 : 184.

FLOWER, W. H. 1879. On the caecum of the red wolf (*Canis jubatus*, Desm.). *Proc. zool. Soc. Lond.* : 766–767.

—— 1880. On the bush dog (*Icticyon venaticus*, Lund). *Proc. zool. Soc. Lond.* : 70–76.

—— 1884. *Catalogue of the specimens illustrating the osteology and dentition of the vertebrated animals contained in the museum of the Royal College of Surgeons of England. Part II Mammalia.* London.

FOX, M. W. 1970. A comparative study of the development of facial expressions in canids ; wolf, coyote and foxes. *Behaviour* (Leiden), **36** : 49–73.

—— 1971. *Behaviour of wolves, dogs and related canids.* London.

—— 1975. *The wild canids ; their systematics, behavioral ecology and evolution.* New York & London.

FRISCH, J. L. 1775. *Das Natur-System der vierfüssigen Thiere.* Golgau : 15.

GARROD, A. H. 1873. Note on the caecum of *Canis cancrivorus*. *Proc. zool. Soc. Lond.* : 748–750.

—— 1878. Notes on the visceral anatomy of *Lycaon pictus* and of *Nyctereutes procyonoides*. *Proc. zool. Soc. Lond.* : 373–377.

GILMORE, R. M. 1946. Mammals in archaeological collections from southwest Pennsylvania. *J. Mammal.* **27** : 227–234.

GIPSON, P. S., SEALANDER, J. A. & DUNN, J. E. 1974. The taxonomic status of wild *Canis* in Arkansas. *Syst. Zool.* **23** : 1–11.

GOLANI, I. & KELLER, A. 1975. A longitudinal field study of the behavior of a pair of golden jackals. *In* Fox (1975) : 303–335.

GOODWIN, H. A. & HOLLOWAY, C. V. 1972. *Red data book I : Mammalia.* Morges, Switzerland.

GOWER, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **53** : 325–338.

—— 1971. A general coefficient of similarity and some of its properties. *Biometrics*, **27** : 857–871.

GRAY, A. P. 1972. *Mammalian hybrids: a checklist with bibliography.* Slough (Commonwealth Agricultural Bureaux).

GRAY, J. E. 1821. On the natural arrangement of vertebrose animals. *London Med. Reposit.* **15** : 296–310.

—— 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families.... *Ann. Phil.* N.S. **10** : 337–344.

—— 1868. Notes on the skulls of the species of dogs, wolves and foxes (Canidae) in the collection of the British Museum. *Proc. zool. Soc. Lond.* : 492–525.

GROVES, C. P. 1971. Request for a declaration modifying Article I so as to exclude names proposed for domestic animals from zoological nomenclature. *Bull. zool. Nom.* **27** : 269–272.

GUILDAY, J. E. 1962. Supernumerary molars of *Otocyon*. *J. Mammal.* **43** : 455–462.

HALL, E. R. & KELSON, K. R. 1959. *The mammals of North America*, vol. 2. New York.

HAMILTON SMITH, C. 1839. *Dogs I.* The naturalists' library, ed. W. Jardine, vol. 18.

HARRISON, D. L. 1968. *The mammals of Arabia*, vol. 2. London.

HELLER, E. 1914. New subspecies of mammals from equatorial Africa. *Smithson. misc. Collns* **63** (7), 1–3.

HERSHKOVITZ, P. 1957. A synopsis of the wild dogs of Colombia. *Noved. colomb.* **3** : 157–161.

—— 1961. On the South American small-eared zorro *Atelocynus microtis* Sclater (Canidae). *Fieldiana zool.* **39** (44) : 505–523.

—— 1972. The recent mammals of the Neotropical Region : a zoogeographic and ecological review. *In* Keast *et al.* (1972) : 311–431.

HILDEBRAND, M. 1952a. An analysis of body proportions in the Canidae. *Am. J. Anat.* **90** : 217–256.

—— 1952b. The integument in Canidae. *J. Mammal.* **33** : 419–428.

—— 1954. Comparative morphology of the body skeleton in Recent Canidae. *Univ. Calif. Publs Zool.* **52** : 399–470.

HOPKINS, G. H. E. 1949. The host-associations of the lice of mammals. *Proc. zool. Soc. Lond.* **119** : 387–604.

HUXLEY, T. H. 1880. On the cranial and dental characters of the Canidae. *Proc. zool. Soc. Lond.* : 238–288.

IMAIZUMI, Y. 1967. A new genus and species of cat from Iriomote, Ryukyu Islands. *J. mammal. Soc. Japan*, **3** : 75–106.

KEAST, A., ERK, F. C. & GLASS, B. 1972. *Evolution, mammals and southern continents.* New York.

KÉLER, S. VON. 1971. A revision of the Australasian Boopiidae (Insecta : Phthiraptera), with notes on the Trimenoponidae. *Aust. J. Zool.* suppl. 6 : 1–126.

KLEIMAN, D. 1966. Scent marking in the Canidae. *In* Jewell, P. A. & Loizos, C. (eds), Play, exploration and territory in mammals. *Symp. zool. Soc. Lond.* **18** : 167–177.

—— 1967. Some aspects of social behaviour in the Canidae. *Am. Zool.* **7** : 365–372.

KRAGLIEVICH, L. 1930. Craneometría y clasificación de los cánidos sudamericanos especialmente los angentinos actuales y fósiles. *Physis.* **10** : 35–73.

KRUMBIEGEL, VON I. 1953. Der "Andenwolf", *Dasycyon hagenbecki* (Krumbiegel, 1949). *Säugetierk. Mitt.* **1** : 97–104.

KÜHME, W. 1965a. Communal food distribution and division of labour in African hunting dogs. *Nature, Lond.* **205** : 443–444.

—— 1965b. Freilandstudien zur Soziologie des Hyänenhundes (*Lycaon pictus lupinus* Thomas, 1902). *Z. Tierpsychol.* **22** : 495–541.

LANGGUTH, A. 1970. Una nueva clasificación de los canidos sudamericanos. *Act. IV Congr. Latin. Zool.* **1** : 129–143.

—— 1975. Ecology and evolution in the South American canids. *In* Fox (1975) : 192–206.

LAWICK-GOODALL, H. & J. VAN. 1970. *Innocent killers.* London.

LAWRENCE, B. & BOSSERT, W. H. 1967. Multiple character analysis of *Canis lupus latrans* and *familiaris*, with a discussion of the relationships of *Canis niger*. *Am. Zool.* **7** : 223–232.

—— —— 1975. Relationships of North American *Canis* shown by a multiple character analysis of selected populations. *In* Fox (1975) : 73–86.

LIDICKER, W. Z. 1973. A phenetic analysis of some New Guinea rodents. *Syst. Zool.* **22** : 36–45.

LITTLE, C. C. 1957. *The inheritance of coat color in dogs.* London.

LÖNNBERG, E. 1916. A remarkable occurrence of the first hind toe in the common fox (*Vulpes vulpes*). *Ark. Zool.* **10** (21) : 1–5.

MACPHERSON, A. H. 1969. The dynamics of Canadian arctic fox populations. *Can. Wildl. Serv. Rep. Ser.* no. 8 : 1–52.

MAJOR, F. 1900. Remarks on remains of *Cyon sardous* from a cave in Sardinia. *Proc. zool. Soc. Lond.* : 833–835.

MARRETT TIMS, H. W. 1896. On the tooth genesis in the Canidae. *J. Linn. Soc.* (Zool.) **25** : 445–480.

MATTHEW, W. D. 1930. The phylogeny of dogs. *J. Mammal.* **11** : 117–138.

MECH, L. D. 1970. *The wolf: the ecology and behaviour of an endangered species.* New York.

MENGEL, R. M. 1971. A study of dog–coyote hybrids and implications concerning hybridization in *Canis*. *J. Mammal.* **52** : 316–336.

MILLER, G. S. 1912. *Catalogue of the mammals of Western Europe in the collection of the British Museum.* London.

—— & KELLOGG, R. 1955. *List of North American recent mammals.* Washington.

MIVART, ST G. 1890. *A monograph of the Canidae.* London.

NEWTON, A. 1868. The secretary on additions to the menagerie. *Proc. zool. Soc. Lond.* : 529.

OGNEV, S. I. 1962. *Mammals of eastern Europe and northern Asia*, vol. 2, *Carnivora* (*Fissipedia*). Israel Program for Scientific Translations. Jerusalem.

OSGOOD, W. H. 1934. The genera and subgenera of South American canids. *J. Mammal.* **15** : 45–50.

—— 1943. The mammals of Chile. *Publs Field Mus. nat. Hist.* (Zool.). **542** : 1–222.

PARADISO, J. L. 1971. A report on the taxonomic status and distribution of the red wolf. *Wildlife* (U.S. Fish & Wildlife Service) no. 145 : 1–36.

—— & NOWAK, R. M. 1972. *Canis rufus. Mammalian Species* no. 22 : 1–4.

PETTER, G. 1964. Origine du genre *Otocyon* (Canidae africain de la sous-famille des Otocyoninae). *Mammalia* **28** : 330–344.

POCOCK, R. I. 1913. The affinities of the antarctic wolf (*Canis antarcticus*). *Proc. zool. Soc. Lond.* : 382–393.

—— 1936. The foxes of British India. *J. Bombay nat. Hist. Soc.* **39** : 36–57.

—— 1938. The jackals of S.W. Asia and S.E. Europe. *Proc. zool. Soc. Lond.* (B) **108** : 37–39.

—— 1941. *The fauna of British India including Ceylon and Burma*, vol. 2. London.

PULLIAINEN, E. 1967. A contribution to the study of the social behaviour of the wolf. *Am. Zool.* **7** : 313–317.

RADINSKY, L 1973. Evolution of the canid brain. *Brain, Behaviour and Evolution.* **7** : 169–202.

RIDE, W. D. L. 1970. *Native mammals of Australia.* Oxford.

ROMER, A. S. 1955. *Vertebrate palaeontology.* Chicago.

SCHENKEL, R. 1967. Submission : its features and functions in the wolf and dog. *Am. Zool.* **7** : 319–331.

SCOTT, J. P. 1967. The evolution of social behaviour in dogs and wolves. *Am. zool.* **7** : 373–381.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.* **85** : i–xvi, 1–350.

SNEATH, P. H. A. & SOKAL, R. R. 1973. *Numerical taxonomy.* San Francisco.

THOMAS, O. 1914. On various South American mammals. *Ann. Mag. nat. Hist.* ser. 8, **13** : 345–363.

—— 1918. Some notes on the small sand-foxes of North Africa. *Ann. Mag. nat. Hist.* ser. 9, **1** : 243–245.

TODD, N. B. 1970. Karyotypic fissioning and canid phylogeny. *J. theor. Biol.* **26** : 445–480.

Trouessart, E. L. 1885. Catalogue des mammifères vivants et fossiles. Carnivora. *Bull. Soc. Etud. Scient. Angers*, **14** : 1–108.

Troughton, E. 1957. *Furred animals of Australia.* Sydney.

Van der Merwe, N. J. 1953. The jackal. *Fauna Flora Pretoria* **4** : 4–77.

Van Wormer, J. 1964. *The world of the coyote.* Philadelphia & New York.

Winge, H. 1924. *Pattedyr-Slaegter, vol.* 2 : *Rodentia, Carnivora, Primates.* Copenhagen.

Woolpy, J. H. & Ginsburg, B. E. 1967. Wolf socialization : a study of temperament in a wild social species. *Am. Zool.* **7** : 357–363.

Juliet Clutton-Brock, Ph.D.
G. B. Corbet, Ph.D.
Department of Zoology
M. Hills, Ph.D.
Department of Central Services
British Museum (Natural History)
Cromwell Road
London SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.)
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepède, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay Recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. Pp. 245; 33 Plates, 47 Text-figures. 1973. £10.80.
5. WHITEHEAD, P. J. P. The Clupeoid Fishes of the Guianas. Pp. 227; 72 Text-figures. 1973. £9.70.
6. GREENWOOD, P. H. The Cichlid Fishes of Lake Victoria, East Africa: the Biology and Evolution of a Species Flock. Pp. 134; 1 Plate, 77 Text-figures. 1974. £3.75.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

5.BM.Z

THE CRANIAL MUSCULATURE AND TAXONOMY OF CHARACOID FISHES OF THE TRIBES CYNODONTINI AND CHARACINI

BRITISH
CENTRAL
26 APR 1976
LIBRARY
NATURAL HISTORY

G. J. HOWES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 4
LONDON: 1976

THE CRANIAL MUSCULATURE AND TAXONOMY OF CHARACOID FISHES OF THE TRIBES CYNODONTINI AND CHARACINI

BRITISH MUSEUM
GENERAL
26 APR 1976
LIBRARY
NATURAL HISTORY

BY

GORDON JON HOWES

Pp 201–248 ; 25 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 4
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 29, *No.* 4, *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Zool.)

ISSN: 0007–1498

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 23 *April,* 1976 *Price* £3.45

THE CRANIAL MUSCULATURE AND TAXONOMY OF CHARACOID FISHES OF THE TRIBES CYNODONTINI AND CHARACINI

By G. J. HOWES

CONTENTS

	Page
SYNOPSIS	203
INTRODUCTION	203
METHODS AND MATERIALS	204
ABBREVIATIONS USED IN TEXT FIGURES	205
TRIBE CYNODONTINI	206
DESCRIPTION OF THE CRANIAL MUSCULATURE	207
Facial musculature	207
Hyoid musculature	216
Muscles of the branchial arches	219
PECTORAL FIN MUSCULATURE	220
FUNCTIONAL MORPHOLOGY	223
TAXONOMIC CONSIDERATIONS	226
The status of the genus *Roestes*	226
Intrarelationships of the Cynodontini	227
TRIBE CHARACINI	229
DESCRIPTION OF THE CRANIAL MUSCULATURE OF *Charax gibbosus*	230
Facial musculature	230
Hyoid musculature	231
Muscles of the branchial arches	233
TAXONOMIC CONSIDERATIONS	233
The genera of the Characini	233
Interrelationships of the Characini	238
Remarks on the genus *Agoniates*	239
DISCUSSION	240
ACKNOWLEDGEMENTS	241
APPENDIX Observations on the cranial anatomy of the cyprinid fish *Macrochirichthys macrochir*	241
REFERENCES	245

SYNOPSIS

The cranial and some other musculature of characoid fishes of the tribes Cynodontini and Characini is described and compared. The tribes are redefined on the basis of myological and associated osteological characters. It is shown that some of these characters are shared specializations which unite the tribes in the subfamily Characinae.

An attempt is also made at a functional description of the jaw mechanism of *Rhaphiodon*.

A remarkable example of parallelism is noted between a cynodontid (*Rhaphiodon*) and a cyprinid fish (*Macrochirichthys*). The cranial musculature of the latter is described.

INTRODUCTION

THROUGHOUT the extensive literature on the Characoidei (see, for example, the bibliography in Gery, 1972b) few references have been made to the myology of these fishes. Those that do make only brief comment on particular features. Of earlier works, that of Grenholm (1923) describes the pectoral girdle muscles of *Salminus* and *Alestes*, Holmquist (1911) the hyoid muscles of *Hydrocynus*, and Nelson (1949) the pectoral muscles of *Rhaphiodon*.

Of more recent work, that of Kampf (1961) deals with the cranial muscles of *Hydrocynus* and presents a functional analysis of the jaw mechanism. Robert's (1969) work on some predatory characoids, although an osteological study, makes reference to some cranial muscles. Winterbottom (1974) has figured and referred to the branchial arch muscles of *Brycon*.

The most comprehensive account to date of comparative myology in the characoids has been that of Alexander (1964). In that work the author describes the cranial muscles of some diverse neotropical genera. Later, Alexander (1965) again commented on the cranial musculature of some characoids when comparing them with siluroids.

This present study is part of a wider ranging one, planned to cover the cranial myology of all major characoid families. A preliminary survey suggested that a more limited study of some 'specialized' predatory taxa might be fruitful in establishing the primitive or advanced nature of certain characters in the skeleto-muscular systems of these fishes and thus provide pointers to phyletic relationships.

Two groups of species are considered in this paper, the Cynodontini and the Characini. These are treated as tribes and the subfamily which they constitute (the Characinae) is restricted to those taxa sharing certain myological and osteological specializations not found in members of the Characinae *sensu* Weitzman (1962) (referred to in this paper as the Tetragonopterinae ; see p. 239). The subfamily name is restricted because of the inclusion of the type genus *Charax* in the tribe Characini (see Myers, 1949).

A remarkable example of parallelism is noted between the characoid *Rhaphiodon* and the cyprinoid *Macrochirichthys*. A description of the cranial musculature of the latter is included as an Appendix to this paper.

METHODS AND MATERIALS

Specimens were dissected on their right side (both sides in some cases). The drawings were made using a Wild M4 and M5 drawing apparatus. Details were added freehand using high power magnification. The drawings were reversed to facilitate comparison with those of other authors.

As well as the material listed below, specimens representing species of all characoid families were dissected.

List of specimens used (all radiographed) :

Species	BMNH register number	Standard length (mm)
Acanthocharax microlepis	1971.10.17:1444–1460	47, 63; alizarin preparation, 62
Asiphonichthys stenopterus	1944.2.29:2	42
Charax gibbosus	1972.7.27:832–846	103–70 (including alizarin preparation, 95)
Charax gibbosus	1878.1.21:6	skeleton
Cynodon gibbus	1972.7.27:43–45	196, 198 ; dry skull
Cynopotamus argenteus	1895.5.17:237	147

Cynopotamus argenteus	1872.6.18:24	skeleton
Cynopotamus goeldii	1912.10.31:20	116
Cynopotamus lineasquamis	1897.11.26:4	150
Cynopotamus magdalenae	1972.7.27:847–854	100, 100, 105 ; alizarin preparation, 80
Exodon paradoxus	Unregistered	55
Genycharax tarpon	1895.11.16:100	78
Gnathocharax steindachneri	1935.1.25:2–4	22
Heterocharax macrolepis	1926.10.27:97–110	43–46
Hydrolycus pectoralis	1927.6.7:4–5	220
Hydrolycus scomberoides	1972.7.27:46–49	190, 197, 203
Hydrolycus scomberoides	1866.8.14:122	skeleton
Hydrolycus scomberoides	Unregistered	dry skull
Macrochirichthys macrochir	1922.5.19:1	400
Macrochirichthys macrochir	1866.5.2:46	216
Macrochirichthys macrochir	1898.11.8:121	skeleton
Opsariichthys uncirostris	1923.3.5:6–12	150
Opsariichthys uncirostris	1901.3.6:9	skeleton
Rhaphiodon vulpinus	1935.6.4:34–39	230 ; alizarin preparation, 93
Rhaphiodon vulpinus	1893.4.24:30–31	325, 305
Rhaphiodon vulpinus	1897.12.1:184	dry skull
Rhaphiodon vulpinus	1881.7.2:17	600
Roeboides dayi	1920.12.20:25–29	90
Roeboides guatemalensis	1909.3.12:11–15	87
Roeboides myersii	Unregistered	115
Roeboides prognathus	1935.6.4:256–65	alizarin preparation, 110
Roestes alatus	1924.3.3:46–48	84–95

ABBREVIATIONS USED IN TEXT FIGURES

Muscles and connective tissues

A_1, A_2a, A_2b, A_3 A_W Divisions of the *adductor mandibulae*

AAP	*Adductor arcus palatini*
ABP	*Abductor profundus*
ABS	*Abductor superficialis*
AD	Accessory depressor muscle
AO	*Adductor operculi*
ARD	*Arrector dorsalis*
ARV	*Arrector ventralis*
DO	*Dilatator operculi*
EPAX	Epaxial muscles
HH	*Hyohyoideus*
H-HT	*Hyohyoideus*-hypohyal tendon
HY-SHT	*Sternohyoideus*-hypobranchial tendon
HY-UT	Hypobranchial-urohyal-*rectus ventralis* tendon
HYPAX	Hypaxial muscles
IM	*Intermandibularis*
LAP	*Levator arcus palatini*
LAT.S	*Lateralis superficialis*
LO	*Levator operculi*
LS-PT	*Lateralis superficialis*-pterotic tendon
OBV 1–4	*Obliqui ventrales*
PH	*Protractor hyoideus*
PHCE	*Pharyngoclavicularis externus*
PHCI	*Pharyngoclavicularis internus*
RC	*Rectus communis*
RV	*Rectus ventralis*
SBA	Swimbladder appendices
SCA	*Supracarinalis anterior*
SH	*Sternohyoideus*
SHD	Dorsal division of *sternohyoideus*
SPO	*Sphincter oesephagi*
TCT	Tendinous connective tissue
TRV	*Transversus ventralis*
VT	Ventral tendon of *adductor mandibulae*

Skeletal elements

bas	Basihyal	Lpma	Ligament connecting the premaxilla with the maxilla
bp	Basihyal projection (thickened tissue)	Lpp	Ligament connecting the preopercle and pterotic
c1–5	Ceratobranchials	Luh	Ligament connecting the urohyal and hypohyal
ce1–6	Centra	max	Maxilla
ch	Ceratohyal	ns	Neural spines
cl	Cleithrum	op	Operculum
cor	Coracoid	pmx	Premaxilla
df	Dilatator fossa	po	Preoperculum
ep	Epihyal	prb	Pleural ribs
hyo	Hyomandibula	ps	Parasphenoid
hyp	Hypohyal	pte	Pterotic
imb	Intermuscular bones	ptt	Post-temporal
io	Interoperculum	rs	Rhinosphenoid
Laep	Ligament connecting the retroarticular and epihyal	q	Quadrate
Laq	Ligament connecting the anguloarticular and quadrate	sc	Supracleithrum
Lihp	Ligament connecting the interhyal and preopercle	sn	Supraneurals
Lmp	Ligament connecting the maxillary and palatine bones	sp	Sphenotic
		sy	Symplectic
		tr	Tripus
		ur	Urohyal

In all drawings muscles are indicated by thin continuous lines, tendons by thin dashes, ligaments by thick parallel dashes and connective tissue by alternating dots and dashes. Bones are indicated by outline or shaded by stippling.

Tribe **CYNODONTINI** Fowler, 1958

Cynodonidi Fowler, 1958
Cynodontinae Eigenmann, 1909
Sarcodacinae (part) Gregory & Conrad, 1938
Rhaphiodontinae Travassos, 1946
Cynodontidae Greenwood *et al.*, 1966

The species belonging to this tribe are characterized by their compressed, tapering bodies which bear minute scales. The ventral midline of the body is markedly keeled. The mouth is obliquely aligned to the horizontal axis of the body. All the teeth are conical, those at the anterior of the lower jaw being enlarged, sabre-like canines. The teeth are arranged in a single row in both jaws and the maxilla is toothed for its entire length.

The pectoral fins are very long, extending to a point just beyond the centre of the standard length. The dorsal fin is short-based (II 10 rays), the anal long-based (*c.* III 35–80 rays).

The overall coloration of the fishes is silver, some species showing dark humeral and caudal blotches and red pectoral, ventral, adipose and caudal fins.

Species are recorded from the Orinoco and Amazon systems; from the Essequibo in Guyana; from Surinam; and from the La Plata–Paraguay systems (Schultz, 1950; Boeseman, 1952). Specimens appear to have been collected from only the larger rivers. Some species grow to large size. Schultz (1950), for example, records a skin of *Rhaphiodon vulpinus* of 690 mm standard length, while a specimen in the British Museum measures 600 mm S.L. Lüling (1972) figured the head of a specimen of *Hydrolycus* sp. estimated to have been at least 1 metre in length.

Eigenmann (1909, 1910) and Regan (1911) both ranked this group of taxa as a subfamily, but neither commented upon its possible relationships with other characoids.

Gregory & Conrad (1938) included the group in their Sarcodacinae on the basis of superficial morphology.

Greenwood *et al.* (1966) recognized the group as a family, but no diagnosis was given.

Gery (1972b) recognized the subfamily Rhaphiodontinae (following Travassos, 1946 ; see below) and noted that it may be related to the Characinae (= Characini in this paper).

The most complete anatomical study made on any cynodontine species was that of Nelson (1949) who studied the internal anatomy of *Rhaphiodon vulpinus*, principally the swimbladder and Weberian apparatus. He also described and figured the skull and pectoral girdle and briefly commented upon the pectoral musculature.

Weitzman (1962) has described part of the Weberian apparatus of *Rhaphiodon* and *Hydrolycus*, and Roberts (1969) has commented upon certain other osteological features of *Rhaphiodon* (see p. 212).

The genera and species have been revised most recently by Schultz (1950) and the nomenclature used in that paper is adopted here.

Some confusion seems to have arisen concerning the correct application of the names *Cynodon* and *Rhaphiodon*. Travassos (1946, 1951–52) has considered the nomenclatural history of these genera and he concluded that *Cynodon* is a *nomen nudum*. Although it is not relevant to debate the nomenclature in a paper of this nature, the name *Cynodon* does appear to be valid (see Whitehead & Myers, 1971 : 496, para. f), and hence the replacement of Cynodontinae by Rhaphiodontinae (Travassos, 1946) is unjustified.

For reasons stated in this paper (p. 226) the genus *Roestes*, previously assigned to the Characinae (*auct.*) is now considered to be a member of the tribe Cynodontini.

Description of the Cranial Musculature

The following myological descriptions are based on specimens of *Cynodon gibbus*, *Rhaphiodon vulpinus*, *Hydrolycus pectoralis* and *H. scomberoides* (Fig. 1A, B & C).

Facial musculature (Figs 2–6)

The *adductor mandibulae* is composed of sections A_1, A_2a, A_2b and A_W. I have considered A_2 to consist of two divisions rather than representing two separate muscles, i.e. A_2 and A_3, because there is a medial exchange of fibres before insertion ; there are no separate tendons of insertion ; and the sites of origin of the muscle are in accordance with it being a single functional unit.

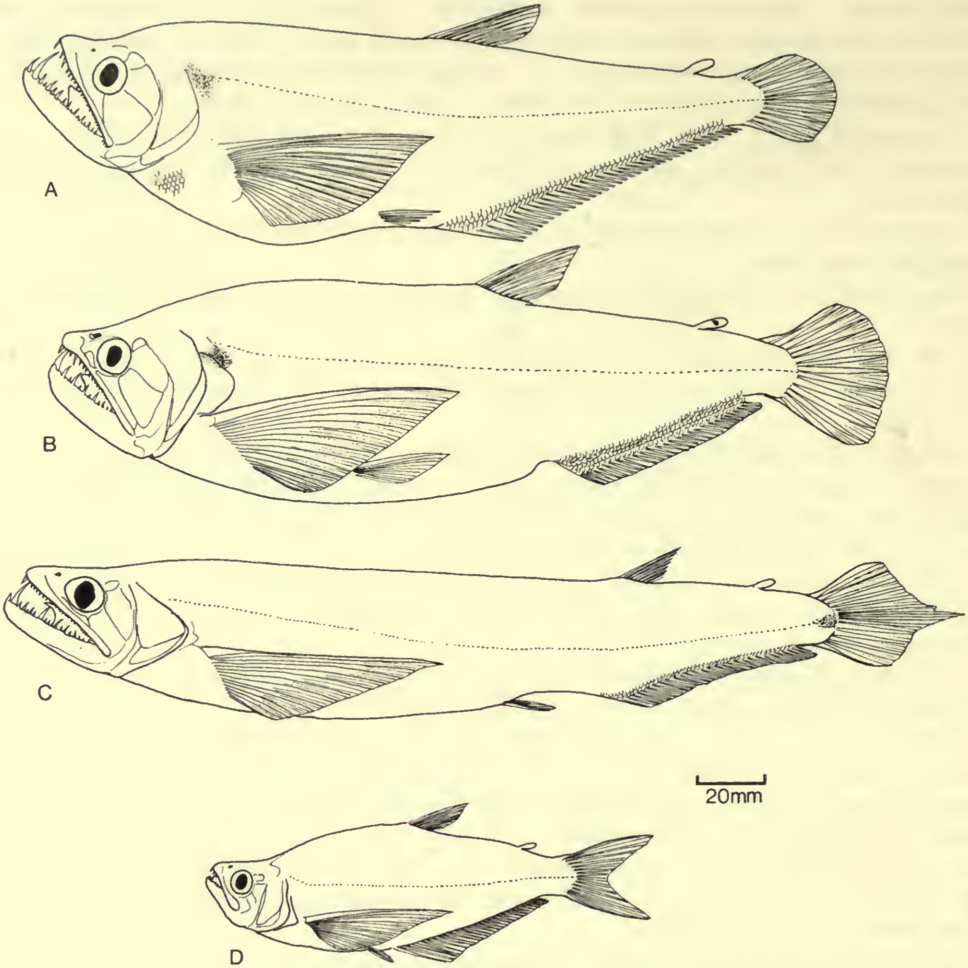


FIG. 1. Outline drawings of (A) *Cynodon gibbus*, (B) *Hydrolycus pectoralis*, (C) *Rhaphiodon vulpinus* and (D) *Roestes alatus*. All drawn to scale.

Alexander (1964) identified the innermost elements of the *adductor mandibulae* in *Hoplias, Serrasalmus, Myleus* and *Leporinus* as A_3. However, I regard the inner division of the muscle in *Hoplias* as A_2b. A 'precursor' of the condition seen in *Hoplias* is found in *Alestes macrolepidotus* (pers. obs.) where a medial element has become separated from the main body of the muscle but lies against the ventromedial surface of the *levator arcus palatini*, seemingly without finding strong attachment to the hyomandibula. I believe that an element in *Leporinus* can also be identified as A_2b. The situation in *Serrasalmus*, however, is more complex and the muscle may well represent A_3. The only other characoid I have examined in which I can definitely define A_3 is *Bivibranchia*, where the muscle has become completely detached from the body of A_2 and runs from the hyomandibula to insert on the ectopterygoid.

Adductor mandibulae section A_1 (Fig. 2). This is a small triangular slip of muscle originating from the ventral edge of the quadrate. The fibres run dorso-anteriorly at an angle of 40° to insert upon the medial dorsal surface of the angulo-articular. Some fibres are seen to pass anteriorly into the extensive band of connective tissue which covers the medial surface of the maxilla and which posteriorly joins the maxilla to the lower jaw. Unlike the condition encountered in other characoids (Bryconini, Alestinae, Hydrocyoninae) there is no separate maxillary-mandibulary ligament (of Alexander, 1964 (= *ligamentum primordiale* of authors)). The 'ligament' is in fact a thickening of the collagenous fibres along the border of that connective tissue which forms a covering to the floor of the orbital cavity, and which extends along the medial face of the maxilla. This arrangement of the tissue allows very little movement of the maxilla (cf. *Charax*, p. 230).

Anteriorly the maxilla is connected to the premaxilla by a short thick ligament (Lpma, Fig. 2). The premaxilla in turn is firmly united to the median ethmoid by a ligament embedded in a sheet of tissue.

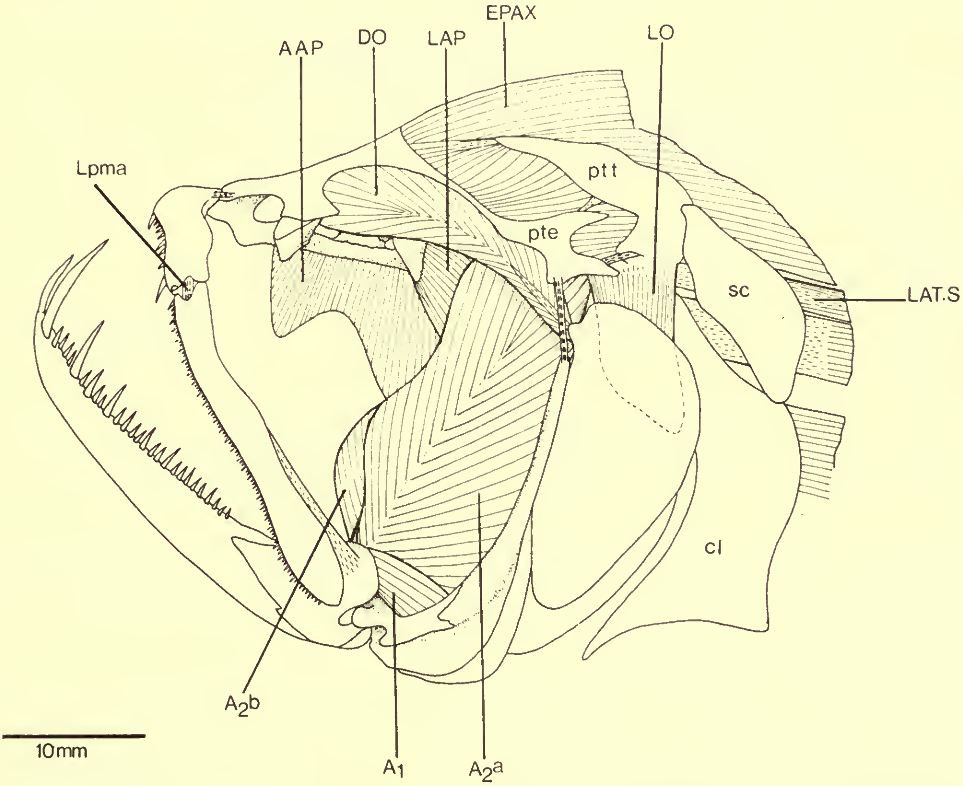


FIG. 2. *Cynodon gibbus*, superficial facial musculature, lateral view. The maxillary has been pulled down to expose the posterior of the lower jaw. The dashed line on the operculum shows the extent of the *levator operculi*.

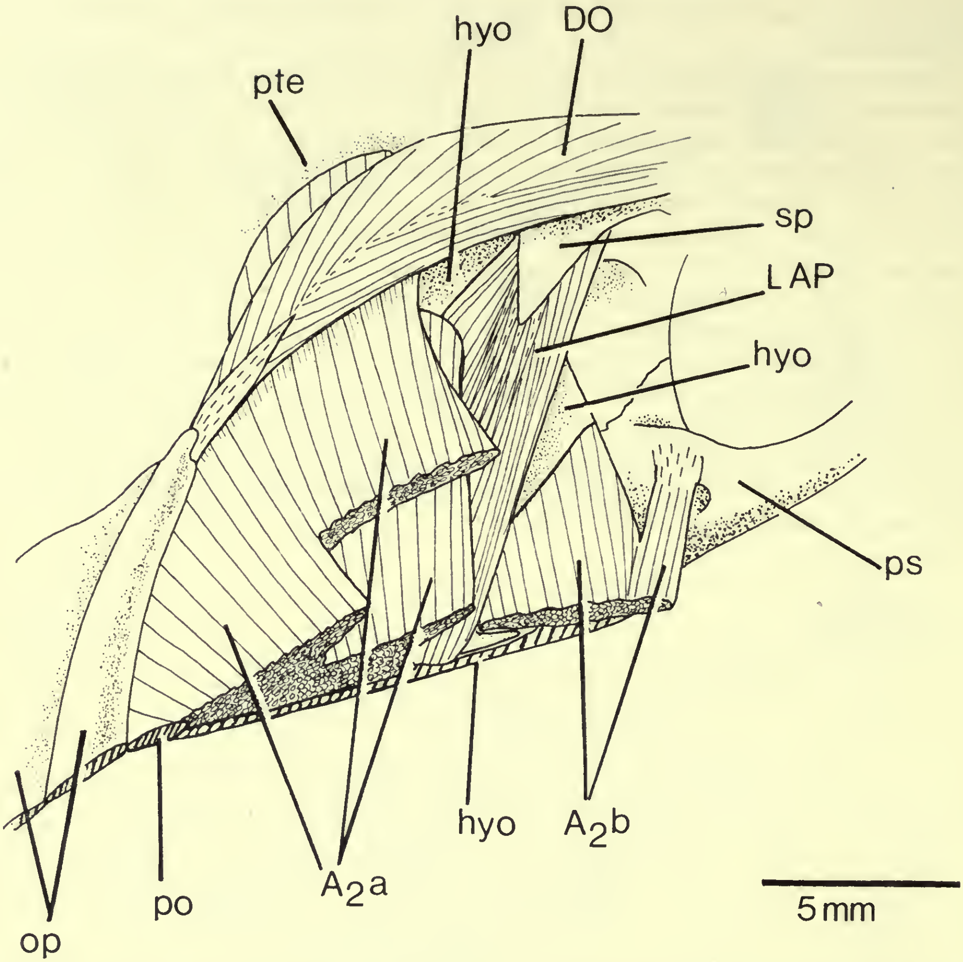


FIG. 3. *Cynodon gibbus*, oblique ventral view of the dorsal section of the *adductor mandibulae* to show its various sites of origin. The muscles and bones have been cut through.

Section A_2 of the *adductor mandibulae* is an extensive and complex element covering the cheek. Dorsally the muscle is divided into outer and inner elements by the *levator arcus palatini*. Between these runs the *ramus mandibularis* V with branches serving both elements.

The outer element (labelled A_2a) takes its posterior origin from the preoperculum, the fibres running ventrally at an angle of 5–40° to insert upon an extensive tendinous sheet which forms the medial face of the muscle. These fibres are met along a medial raphe by those stemming from the pterotic and which run almost perpendicularly (Fig. 3). Medially the muscle has a third point of origin, from the dorso-lateral aspect of the hyomandibula. These fibres also run vertically to insert with those originating from the pterotic. Thus, although at first sight the lateral face of the muscle appears to be formed of two discrete parts, close examination reveals that there is a continual interchange of fibres along the raphe. The orbital face of the muscle is curved in the shape of a shallow S.

Ventrally, a tendon (VT, Fig. 4) runs from the preoperculum, at the point of the quadrato-preopercular suture, to join the aponeurotic system. The more medial ventral fibres of the muscle insert into this tendon. (The tendon is variously developed in the characoids and is most highly so in those long-jawed forms (Hepsetidae, Salminae and Erythrininae) where the *adductor mandibulae* is extensive (pers. obs.)).

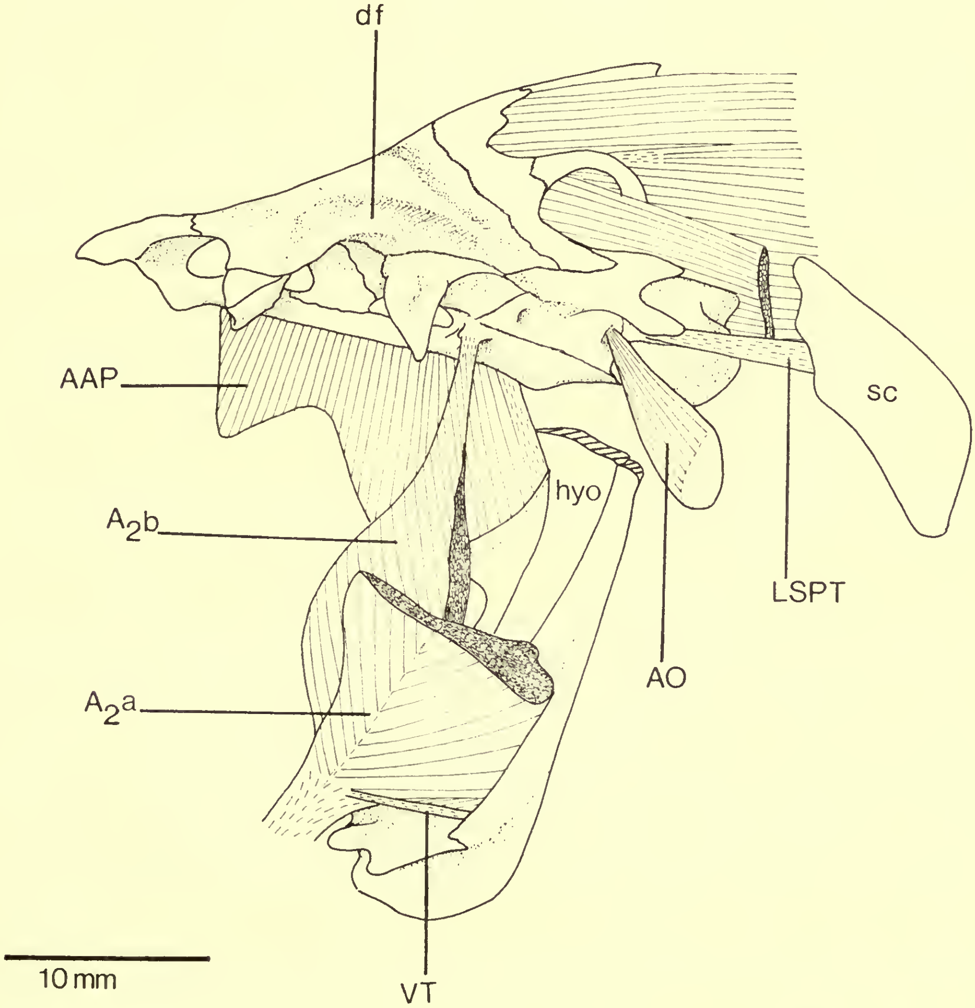


FIG. 4. *Cynodon gibbus*, deeper facial musculature, lateral view. The *adductor mandibulae* has been cut through to show the entire *adductor arcus palatini*. The superficial epaxial musculature has been removed.

The inner element (labelled A_2b) originates posteriorly from the dorso-lateral aspect of the hyomandibula and anteriorly from the lateral wing of the parasphenoid (Figs 3 & 4). The anterior origin is somewhat tendinous and involves only a thin segment of the muscle.

A_2b is separated from A_2a by the interposition of the *levator arcus palatini.* Immediately below this separation, however, the two elements are closely applied. A_2b becomes greatly thickened ventrally and its antero-dorsal margin curved around the orbit to lie in the same plane as A_2a. The epimysial tissue covering the surface of A_2b grades into a thicker (? collagenous) tissue at the leading edge of the muscle; this wraps around the lower margin of the ectopterygoid and covers the inner face of the suspensorial bones, extending across the metapterygoid-quadrate fenestra. Roberts (1969 : 417) remarks that the metapterygoid-quadrate fenestra is lacking in *Rhaphiodon* but is replaced by a thin translucent sheet of bone. In the specimens I have examined the fenestra has always been present. It may be that in some cases there is an extreme thickening of the 'collagenous' tissue covering this opening.

A_2a and A_2b merge together into the aponeurotic sheet. The aponeurosis is complex; medially that part of the sheet which derives from A_2b extends as a thick tendon into the lower jaw to lie perpendicularly across the angulo-articular (Fig. 5).

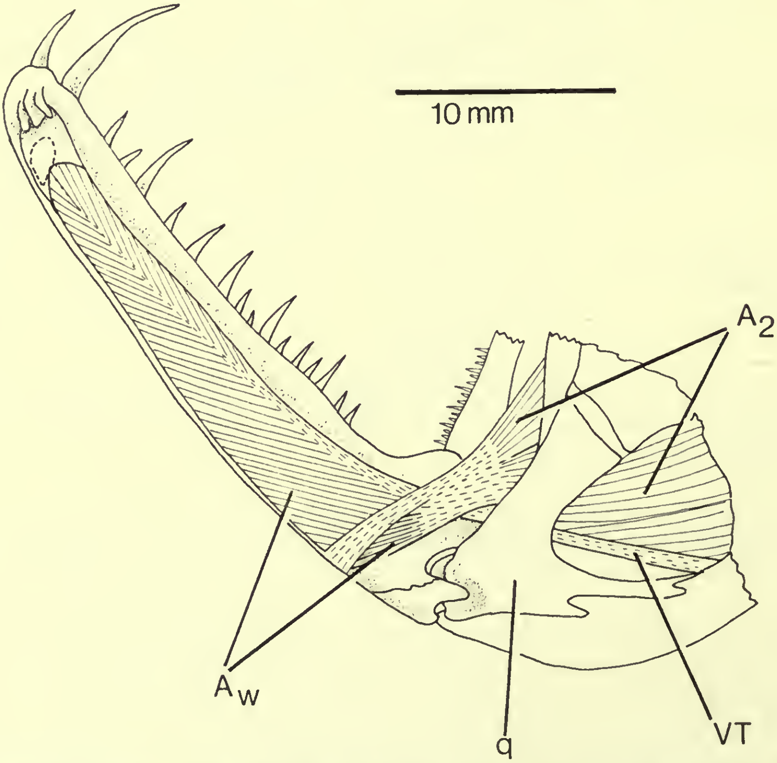


FIG. 5. *Cynodon gibbus*, lower jaw musculature, medial view. The dotted line indicates the position of the *intermandibularis.*

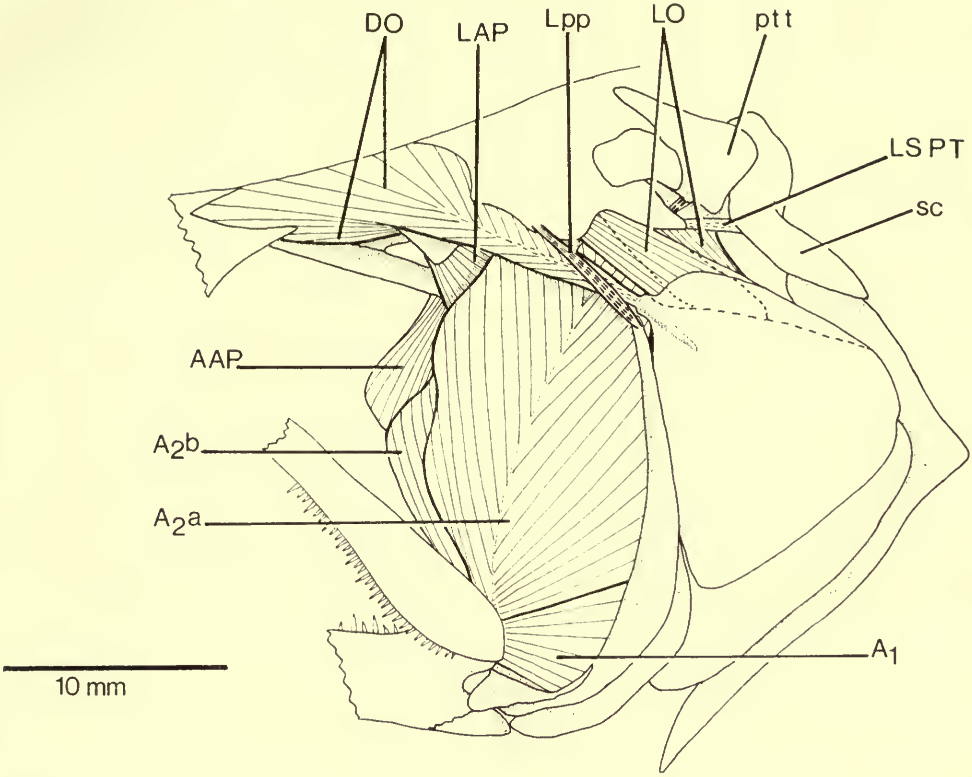


FIG. 6. *Rhaphiodon vulpinus,* superficial facial musculature, lateral view. The long dashed line on the operculum shows the extent of the *levator operculi* ; the short dashed line indicates that of the *adductor operculi.*

It provides the posterior border for the fibres of the *adductor mandibulae* section A_w. Lying laterally to this extension, at an angle of 45° and stemming from A_2a, is another tendon, from which arises another series of fibres contributing to A_w ; these pass laterally and converge with the main mass of the muscle. The dorsal border of A_w is formed by a long tendon originating from the aponeurotic sheet and running along the ventral border of the thick tooth trench. Anteriorly it descends, dividing the muscle. The fibres vary in alignment to the horizontal body axis from 10° to 30°.

The form of the *adductor mandibulae* is almost identical in *Cynodon* (Fig. 2), *Rhaphiodon* (Fig. 6) and *Hydrolycus.* The same complexity of origins and insertions is apparent.

In all genera the hyomandibular bone is reduced, as compared with that in other characoids. That is to say, instead of the bone being in the form of a compressed plate-like element it is reduced to a slender strut (Fig. 7).

In *Cynodon* the hyomandibula exhibits a lateral flange and it is this border which provides the site of attachment for the *adductor mandibulae* A_2a, A_2b stemming from the medial aspect of the bone (see p. 240). In *Rhaphiodon* and *Hydrolycus* the

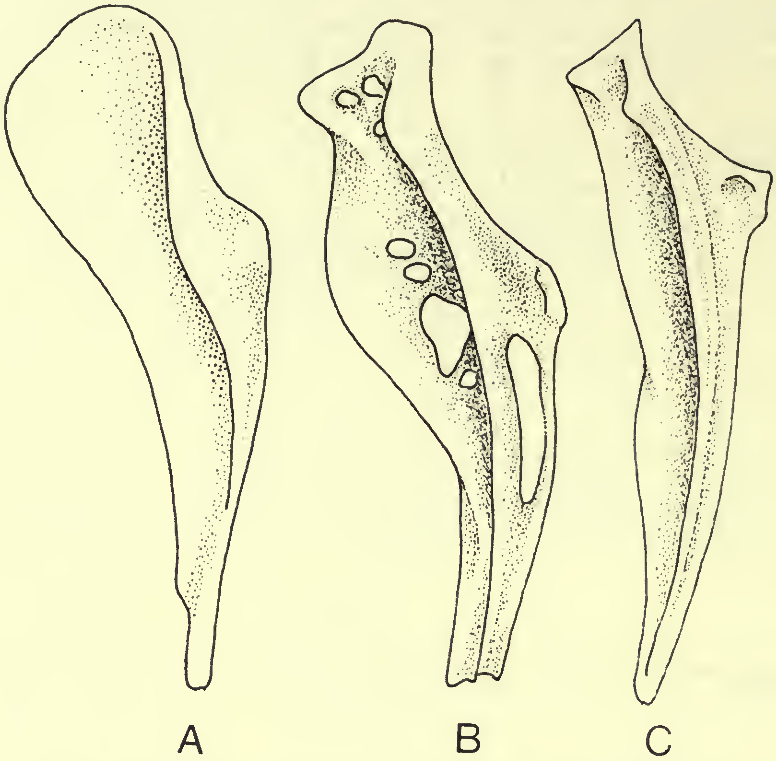


FIG. 7. Hyomandibular bones of (A) *Cynodon gibbus*, (B) *Rhaphiodon vulpinus* and (C) *Hydrolycus scomberoides*. Drawn to same size.

hyomandibula is similarly modified. However, in *Hydrolycus* the lateral flange is curved to face anteriorly, whilst that of *Rhaphiodon* displays a condition somewhat intermediate between those seen in the other two genera (Fig. 7).

Levator arcus palatini (LAP, Figs 2 & 6). This is a large pyriform muscle, the apex of which originates from the sphenotic process. The anterior bundles of fibres originate from long tendons. Insertion is upon the face of the hyomandibula between the two elements of the *adductor mandibulae* A_2. In *Cynodon* some posterior fibres of the *levator* merge with those of both A_2a and A_2b.

The degree of development and orientation of the muscle are about equal in *Cynodon, Rhaphiodon* and *Hydrolycus.*

Adductor arcus palatini (AAP, Figs 2, 4 & 6). In *Cynodon* this muscle originates along the length of the parasphenoid (Figs 2 & 4) to insert ventrally upon the dorsolateral aspects of the endopterygoid. Latero-posteriorly the muscle is covered by the *adductor mandibulae* A_2b. Its posterior margin is bordered by a wide tendon and the muscle inserts into a shallow depression on the hyomandibula.

In *Rhaphiodon* and *Hydrolycus* the origin of the muscle is confined to the posterior part of the parasphenoid (Fig. 6). In all genera a thick band of collagenous fibres runs along the medial face of the endo- and ectopterygoid bones. This tissue is an extension of that which covers the base of the parasphenoid and serves to attach the suspensoria to the lateral margins of that bone.

Levator operculi (LO, Figs 2 & 6). This is a compressed trapezoidal element originating anteriorly from the pterotic. Laterally and posteriorly the fibres take their origin from a horizontal tendon (LS-PT, Figs 4 & 6). (This tendon is not to be confused with the ligament which joins the posttemporal with the intercalar and which lies just medial to it (Figs 2 & 6).) This tendon is the termination of the *lateralis superficialis* of the body musculature. It passes across the medial surface of the supracleithrum to which it is attached by connective tissue, to insert finally on the posteriorly directed pterotic process.

In *Rhaphiodon* the exposed opercular section of the tendon is long (Fig. 6). In *Cynodon* and *Hydrolycus* it is short and thick and provides a face of origin for only a few of the muscle fibres, the remainder stemming somewhat tendinously from the outer surface of the post-temporal. Insertion of the muscle is medially along the dorso-posterior surface of the operculum. In *Rhaphiodon* the muscle extends as a crescent some way around the posterior margin of the operculum (Fig. 6).

Adductor operculi (AO, Fig. 4). The origin of this muscle, through a rather thin tendon, is from the subtemporal fossa which lies on the exoccipital just anterior to the lagenar capsule. The fossa is shallow and is barely visible in a large skull of *Rhaphiodon* (90 mm in length).

The muscle takes the form of a rather compressed cone and is directed laterally at an angle of about 10° to the perpendicular. The area and position of insertion vary in different genera. In *Cynodon* it inserts into the centre of the *levator operculi*, whereas in *Hydrolycus* it runs somewhat anteriorly to the *levator*. In *Rhaphiodon* the *adductor* covers a wide area of insertion following that of the *levator*.

Although both the *adductor* and *levator operculi* insert together, the fibres do not become confluent but retain their identity to their points of insertion.

Dilatator operculi (DO, Figs 2 & 6). In all three genera this muscle has two origins. One is dorsally from the frontal-sphenotic groove or fossa which extends on to the cranial roof ; the other is ventrally from the deep cavity which lies between the frontal and the orbitosphenoid.

In *Hydrolycus* some ventral fibres of the muscle also take their origin from the sphenotic process.

The muscle is asymmetrically bipinnate, the tendon of insertion running close to the ventral border. The anterior and ventral fibres are long and are directed into the raphe at a shallow angle. Those stemming from the dorso-posterior borders are short and acutely angled. The tendon is thickened at its insertion upon the anterior dorsal process of the operculum.

In *Rhaphiodon* the insertion is into a bony tube formed along the lateral face of the operculum (Fig. 6).

In *Cynodon* a well-developed frontal ridge forms the anterior and lateral borders of the dilatator fossa. In *Rhaphiodon* the borders are less well defined being formed medially by the edges of the frontal fontanel.

The *dilatator operculi* is most highly developed in *Rhaphiodon* where it covers the entire frontal area (Fig. 6).

In all species the muscle is covered only by the skin of the head.

The preoperculum is connected to the pterotic by a thick ligament (almost ossified in some specimens). The ligament passes over the *dilatator operculi* and obscures its point of insertion on the operculum.

Hyoid musculature (Figs 8–10)

In all genera the hyoid musculature is of almost identical arrangement.

Protractor hyoidei (PH, Fig. 8). This muscle extends from the second, third and fourth branchiostegal rays to cover the ceratohyal and part of the epihyal. The *protractor hyoidei* of each side passes over the first branchiostegal rays to unite with its counterpart into a single unit running anteriorly to insert dorsally and ventrally to the *intermandibularis*.

The medial, unpaired part of this muscle is divided by a λ-shaped myoseptum. The two latero-dorsal bundles insert via fine tendons into the skin covering the floor of the mouth ; the single ventral bundle is flattened towards its insertion which is by means of two thin, laterally placed tendons attaching to the dentaries on either side of the symphysis.

Dorsally, at the point where the two lateral sections of the muscle join into the single, medial element, there arises a large area of connective tissue which extends to cover the basihyal. Anteriorly the tissue becomes thickened, forming a prominent projection (bp, Fig. 8). Widely spaced, possibly elastin, fibres can be detected in this tissue. Below this layer is another which is closely bound to the basihyal and which joins that element to the hypohyals. This deeper layer is much denser, and the fibres running from the face of the hypohyals appear to be somewhat tendinous.

Intermandibularis (IM, Fig. 8). This muscle is thick, and oval in cross-section. The form of this muscle is almost identical in all three genera.

Hyohyoidei (HH, Fig. 8). The elements of this muscle are weakly developed (the term 'weak' is used here to denote the condition as compared with that in most Cyprinoidei and Siluroidei (Takahasi, 1925 ; Matthes, 1963 ; Winterbottom, 1974 ; pers. obs.)). This degree of development is not only characteristic of the Cynodontini but is evident throughout the Characidae, Hemiodontidae, Erythrininae and in the long-jawed predatory groups, Acestrorhynchinae, Ctenoluciidae and Hepsetidae. However, in other characoid families such as the Prochilodontidae, Anostomatidae and Curimatidae, the *hyohyodei* is more complexly arranged and well developed (pers. obs.).

In many teleosts two sections of this muscle are generally recognized (Millard, 1966 ; Osse, 1969 ; Winterbottom, 1974). However, in the Cynodontini (and in some of the other taxa mentioned above) the division appears to be rather arbitrary and one based on topographical, rather than anatomical grounds (although, of course, a functional difference cannot be ruled out).

The origin of each division is from a short tendon attached to the ventral hypohyal of the opposite side, the tendons crossing antero-ventrally to the hypohyals. This entire site is covered with a connective tissue sheet that extends from the basihyal ; it is, in fact, a continuation of the tissue that connects the basihyal and the *protractor hyoidei* (see above, p. 224 and Fig. 8).

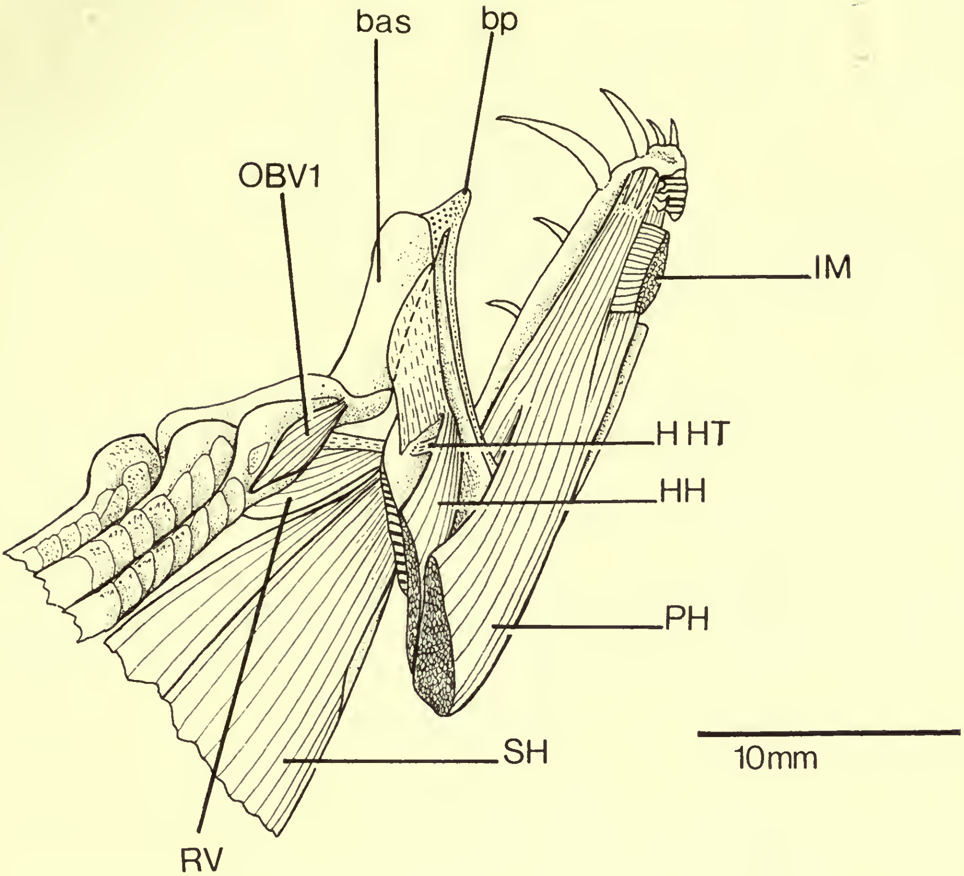


FIG. 8. *Cynodon gibbus*, hyoid musculature, dorso-lateral view. The hypohyal, *protractor hyoideus* and *hyohyoideus* have been cut through. The basihyal is shown entire but the tissue and process anterior to it have been cut along the midline.

The *hyohyoidei* is separated from the *protractor hyoidei* by a thin fascia of tissue as it passes on to the ceratohyal and between the branchiostegal rays. The fibres are closely applied to the branchiostegal membrane, the number of fibres gradually diminishing as the muscle extends from one branchiostegal ray to the next.

The muscle extends from the fifth branchiostegal ray on to the medial face of the suboperculum.

Sternohyoideus (SH, Figs 8, 9 & 10). This is a deep narrow muscle, the posterior limits of which are difficult to define. There is an abrupt change of fibre direction and a feeble myoseptum below the leading edge of the cleithral limb which would appear to mark the anterior limit of the body musculature. (In Cynodontini, however, this is not *hypaxial* body musculature but the *abductor superficialis* of the pectoral girdle ; see Figs 9 & 10, also p. 221.)

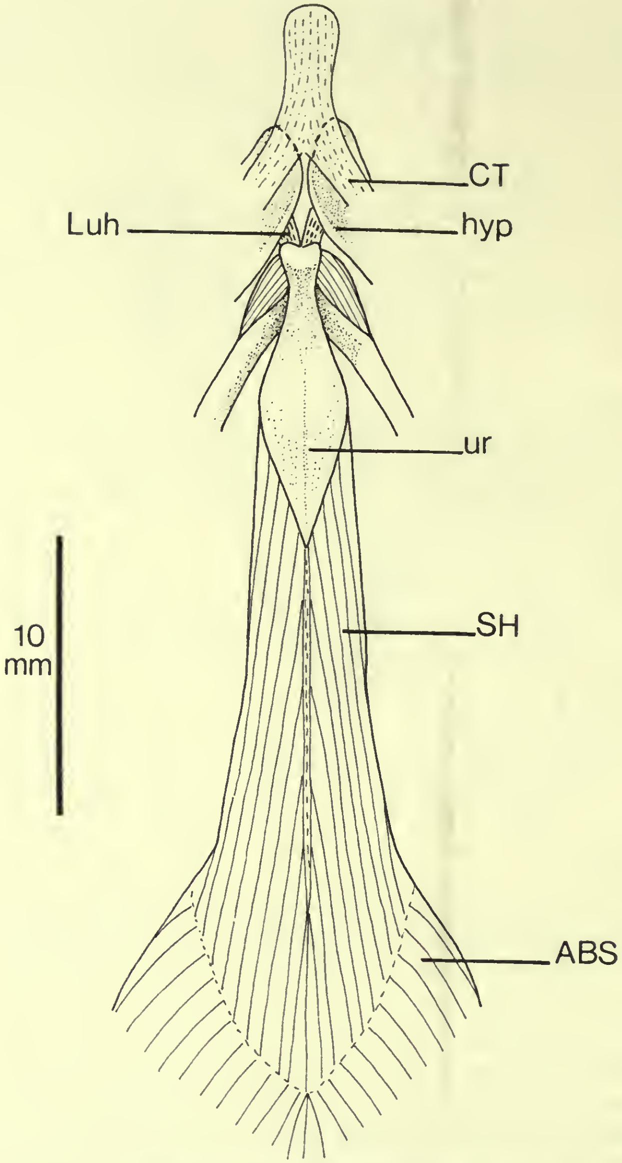


FIG. 9. *Cynodon gibbus, sternohyoideus*, ventral view.

In *Rhaphiodon* the myoseptum between the muscle is a more evident barrier than in *Cynodon* or *Hydrolycus*.

Dorsally, the *sternohyoideus* is divided. The dorsal element (SHD, Fig. 10) extends from the anterior edge of the cleithrum to insert principally through a long tendon running to the tip of the urohyal. Laterally, however, some fibres insert directly on to the lateral face of the urohyal. Posteriorly, fibres run into the main ventral mass of the *sternohyoideus*.

Among the characoids this dorsal separation of the muscle appears to be shared only by members of the Characini (p. 232). Winterbottom (1974 : 270) records such an element in gobiids (after Dietz, 1914) and triacanthiids, and applies the name *sternobranchialis* to this muscle. However, I have refrained from identifying this muscle in characoids until a more adequate survey is made of its occurrence in other teleosts and a definite homology thereby established.

The fibres of the main part of the *sternohyoideus* run antero-dorsally to insert upon the lateral face of the urohyal. The entire muscle is very tendinous. No myosepta appear to be differentiated. Ventrally the muscle is delimited by a strong tendon which runs from the posterior edge of the expanded ventral surface of the urohyal.

Muscles of the branchial arches (Fig. 10)

No previous comparative study of the branchial arch musculature in the characoids has been attempted, although Winterbottom (1974) illustrated and commented upon certain aspects of this musculature system in *Brycon guatemalensis* and the dorsal and ventral branchial arch muscles of *Hydrocynus* were described and figured by Kampf (1961).

The arrangement in the Cynodontini is basically as in *Brycon*, and a provisional survey of branchial arch myology in representative species of various characoid families (pers. obs.) suggests relative uniformity throughout the group. However,

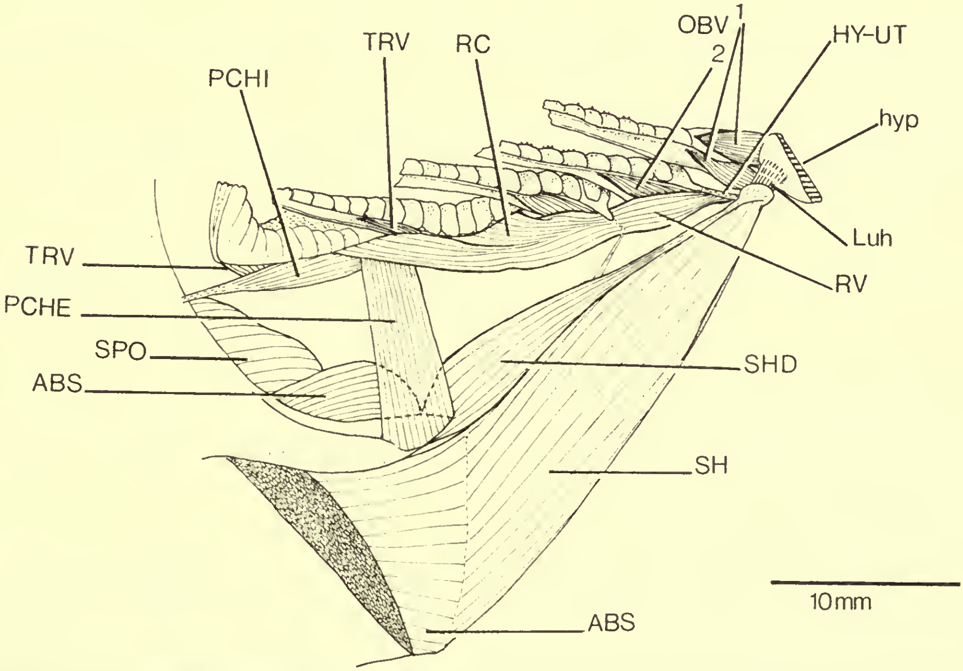


FIG. 10. *Cynodon gibbus*, ventral branchial arch and hyoid musculature, lateral view. The hypohyal has been cut through and moved out of position.

some specializations have been found in those taxa with epibranchial organs (*Chilodus*, *Anodus*).

The following observations were made on the branchial muscles of the Cynodontini.

Obliqui ventrales (OBV1–4, Fig. 10). These are present on the first, second and third gill arches ; that on the first is divided into two elements, one being applied to the leading edge of the ceratobranchial and the hypobranchial, the other placed ventrally.

Rectus ventralis (RV, Fig. 10). This is a thick muscle interconnecting the second and third hypo- and ceratobranchials. The muscle stems from the fascia of tissue which forms a barrier between it and the *rectus communis* (RC). Insertion is into a tendon which runs from the anterior edge of the second hypobranchial to insert into the tip of the urohyal (HY-UT, Fig. 10).

A very thin tendon runs ventrally from the medial surface of the third hypobranchial to pass into the dorsal division of the *sternohyoideus* (see p. 000).

Rectus communis (RC, Fig. 10). This muscle extends from the third hypobranchial to connect with the fourth ceratobranchial and finally to insert along the fifth ceratobranchial.

Transversi ventrales (TRV, Fig. 10). These connect each fourth and fifth ceratobranchials across the midline.

Pharyngoclavicularis externus (PHCE, Fig. 10). This muscle originates from the lower limb of the cleithrum to lie close against the surface of the *abductor superficialis*. It inserts on the fifth ceratobranchial medially to the *rectus communis*.

Pharyngoclavicularis internus (PCHI, Fig. 10). This originates via a long tendon from the anterior edge of the cleithrum and inserts on the fifth ceratobranchial medially to the *rectus communis*.

An examination of the muscles serving the dorsal branchial elements has revealed little difference between the condition in these species and that in *Brycon guatemalensis* as figured and partly described by Winterbottom (1974).

Pectoral Fin Musculature

(Fig. 11)

Although this study is primarily concerned with the cranial muscles, the pectoral muscle system appears to be so extraordinary, and seemingly plays such an important part in the functioning of the jaws (see p. 224), that some elements of the system are described.

In all genera of Cynodontini the coracoids are extensive, thin sheets of bone, closely applied to each other along the midline. Nelson (1949) states that in both his specimens of *Rhaphiodon vulpinus* the major part of the coracoid plate was formed by '. . . one of the coracoid pair, the other being fused to the first proximally' (which I take to mean along the dorsal margin of the bone). I have not found this condition in the specimens of *Rhaphiodon* and *Hydrolycus* I have examined, the two coracoids always being fully developed. It is possible, of course, that such fusion

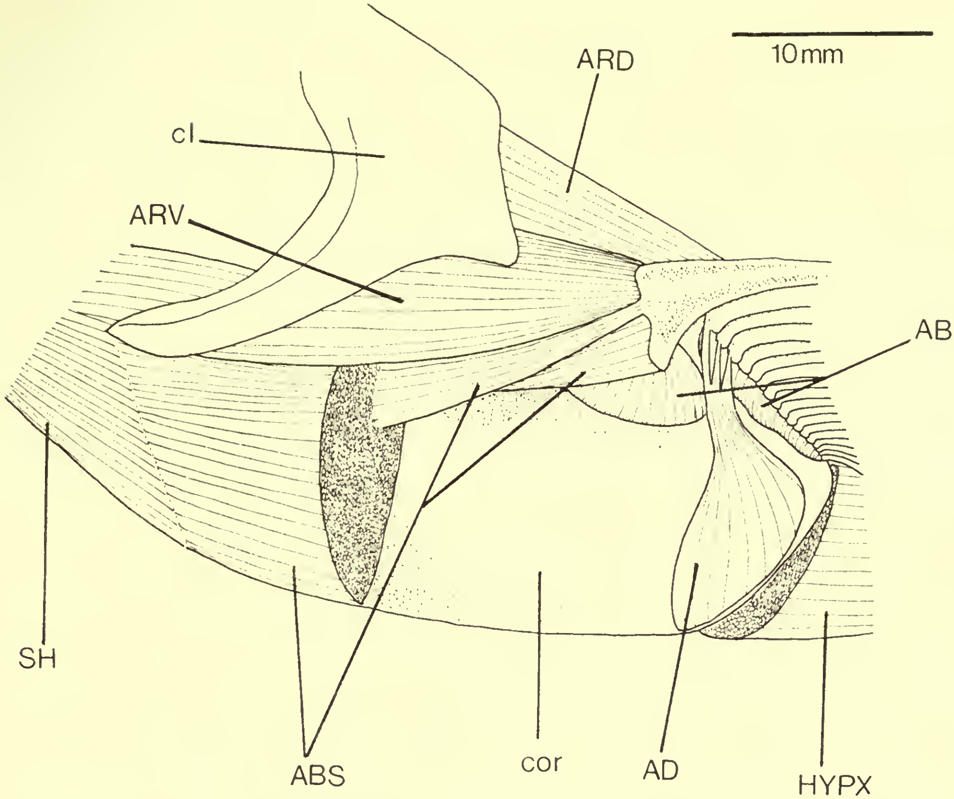


FIG. 11. *Cynodon gibbus*, pectoral fin musculature, left lateral view. The *abductor superficialis* has been cut through leaving intact only those segments that run to the first ray.

occurs in large individuals; unfortunately, Nelson did not state the size of the specimens at his disposal.

The lateral faces of the coracoids provide sites of origin for the extensive *abductor superficialis* muscle (ABS, Fig. 11) which originates as a thick bundle of fibres curved around the anterior edge of the coracoid.

When the jaws are almost closed this part of the muscle can be seen protruding into the branchial cavity.

Applied to the posterior lateral face of the coracoid and lying medially to the *abductor superficialis* there is a triangular sheet-like muscle. The apex of this element inserts via long tendons on the bases of the second, third and fourth pectoral fin rays (AD, Fig. 11).

This muscle has not previously been described for this tribe (Nelson, 1949) and I have been unable to locate it in any other characoid I have examined. Nor, as far as I am aware, has it been described in other teleosts exhibiting a similar pectoral girdle (i.e. *Pantodon, Osteoglossum*; see Greenwood & Thomson, 1960). The function of this element would appear to be that of a depressor (see below, p. 224). It is perhaps a derivative of the *abductor superficialis*.

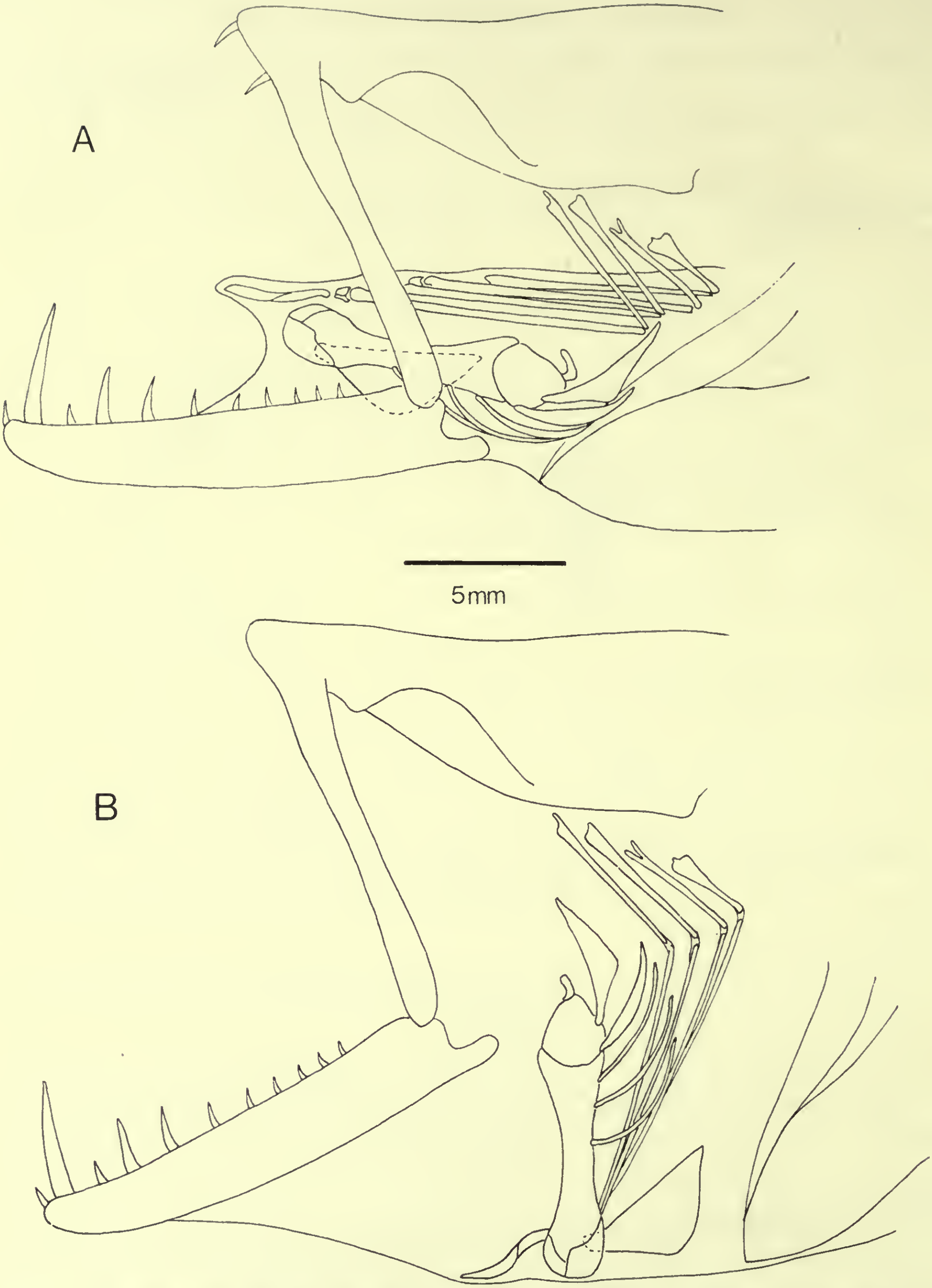


FIG. 12. *Rhaphiodon vulpinus,* outline drawings (made from an alizarin preparation) to show the positions of the hyoid bones when (A) the mouth is half-closed and (B) fully opened. That part of the urohyal obscured by overlying bones is indicated by a dashed line.

Functional Morphology

(Figs 12, 13 & 14)

There do not appear to be any published observations on the feeding behaviour of any members of the Cynodontini. All species seem to be piscivorous; examinations of stomach contents have revealed remains of a characoid (? Hemiodontidae) and cichlids (genera indet.; pers. obs.).

It is of course recognized that the reconstruction of muscle function from the manipulation of preserved material is a hazardous procedure, and that interpretations derived from such observations must be considered highly speculative. Nevertheless, an attempt is made here to reconstruct the possible sequence of movements made by certain parts of the body when the fish (*Rhaphiodon*) is feeding.

In lateral view, the mouth is capable of at least a 90° gape (Fig. 12). The outer surface of the mandibular-suspensorial joint is covered with collagenous tissue. There is a short lateral quadrato-articular ligament embedded within this tissue. Medially there lies a similar ligament (Laq, Fig. 13). From the retro-articular a

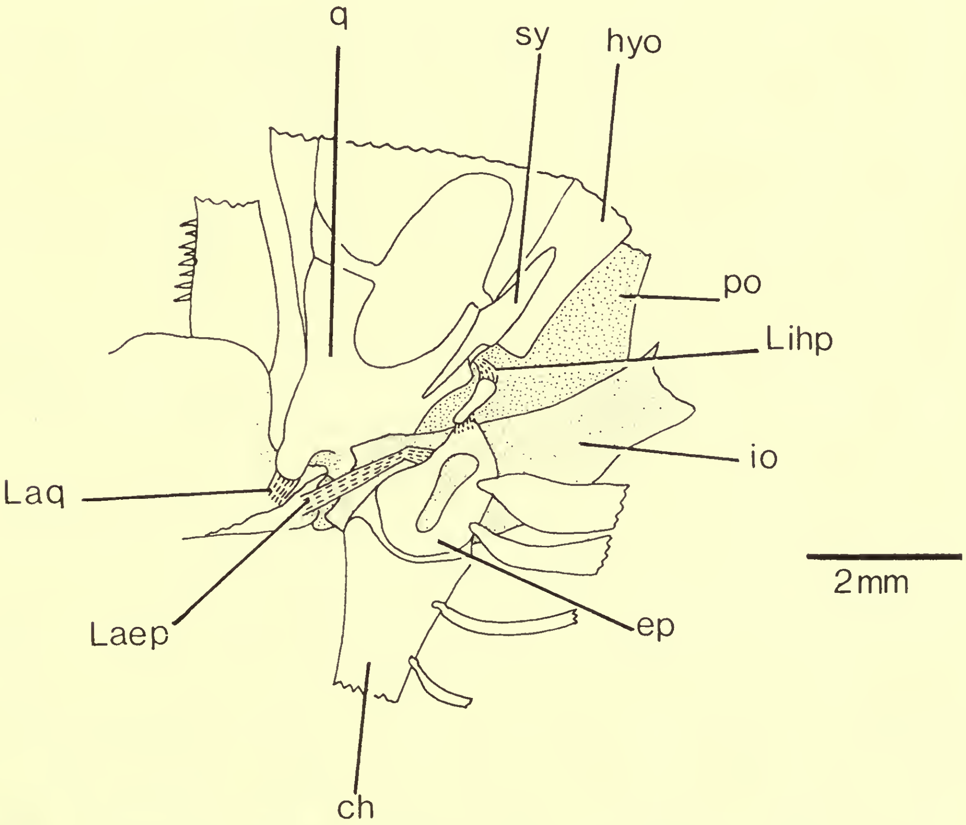


FIG. 13. *Rhaphiodon vulpinus*, ligamentous system of the lower jaw, medial view, right side. The interorbital is indicated by fine stippling, the preoperculum by coarse stippling.

ligament runs dorso-caudally to become applied to the interoperculum. From this point of attachment it is directed somewhat medially to insert upon the lateral face of the epihyal (Laep, Fig. 13). The interhyal is joined by a short ligament to the operculum (Lihp, Fig. 13).

The dentaries are joined at the symphysis by a complexly convoluted hinged joint ('knuckle' joint of Nelson, 1949). Although in preserved material this joint appears to be a rigidly fixed unit, in life no doubt it is capable of allowing the dentaries a substantial degree of lateral movement about this point (Nelson, 1949).

The ligamentous system suggests the capability of an extensive rotation of the dentaries at the quadrate joint and further implies a large abduction of the suspensoria which would force the dentaries widely apart (see Osse, 1969 : 376, concerning observations on the Pike-perch, *Stizostedion*).

A possible sequence in the feeding action may be as follows. As the fish closes upon its prey the mouth is already partly open ; the large pectoral fins are extended laterally, acting as a brake (Nelson, 1949 : 508) ; possibly the small accessory *abductor superficialis* muscle described earlier (p. 221) acts as a depressor and holds the fin rays firmly in position. Contraction of the main *abductor superficialis* and of the ventral *hypaxial* muscles pulls the coracoid ventro-posteriorly and serves to reinforce the contraction of the *sternohyoideus*. The urohyal is moved into a horizontal position (Fig. 12B), the buccal cavity is enlarged by the removal of the hyoid bars into a ventral position ; the 'elastic' connective tissue surrounding the basihyal and extending between the *protractor hyoideus* and the dentaries is everted to form a pouch.

To what degree there is an upward movement of the neurocranium I am unable to ascertain. At rest the skull is aligned in a tilted position to facilitate maximum gape, that is, unlike the situation in the superficially similar stomiatoid *Chauliodus* described by Tchernavin (1953), where there is some considerable upward movement of the cranium into a suitably inclined position when the fish 'strikes' its prey. Strong tendinous attachments of the *epaxial* musculature to posterior parts of the cranium and the development and arrangement of many long intermuscular bones suggest some degree of movement. In *Rhaphiodon* numerous intermuscular bones (*c.* 80–90) are arranged in the *epaxialis* (imb, Fig. 14). The bones are aligned at angles of between 10° and 20° to the horizontal. Their dorsal ends are split into three or four branches. The epaxial muscle fibres are arranged at similar angles but in the opposite direction. Anteriorly the intermuscular bones lie almost horizontal to the body axis and they stem as a bundle from the pterotic.

A further series of Y-shaped bones (epineurals) are found arranged along the bases of the neural spines and embedded in the *lateralis superficialis* (LAT.S, Fig. 14). This latter muscle is a discrete, thick band well separated dorsally from the *epaxialis*. The outer layers of fibres are arranged horizontally, the deeper layers are aligned diagonally. Ventrally, the muscle is not clearly differentiated from the hypaxial body musculature.

Neither *Cynodon* nor *Hydrolycus* display such a marked differentiation of the *epaxialis* from the *lateralis superficialis* as is seen in *Rhaphiodon*, and neither do they possess the numerous intermuscular bones of the *epaxialis*.

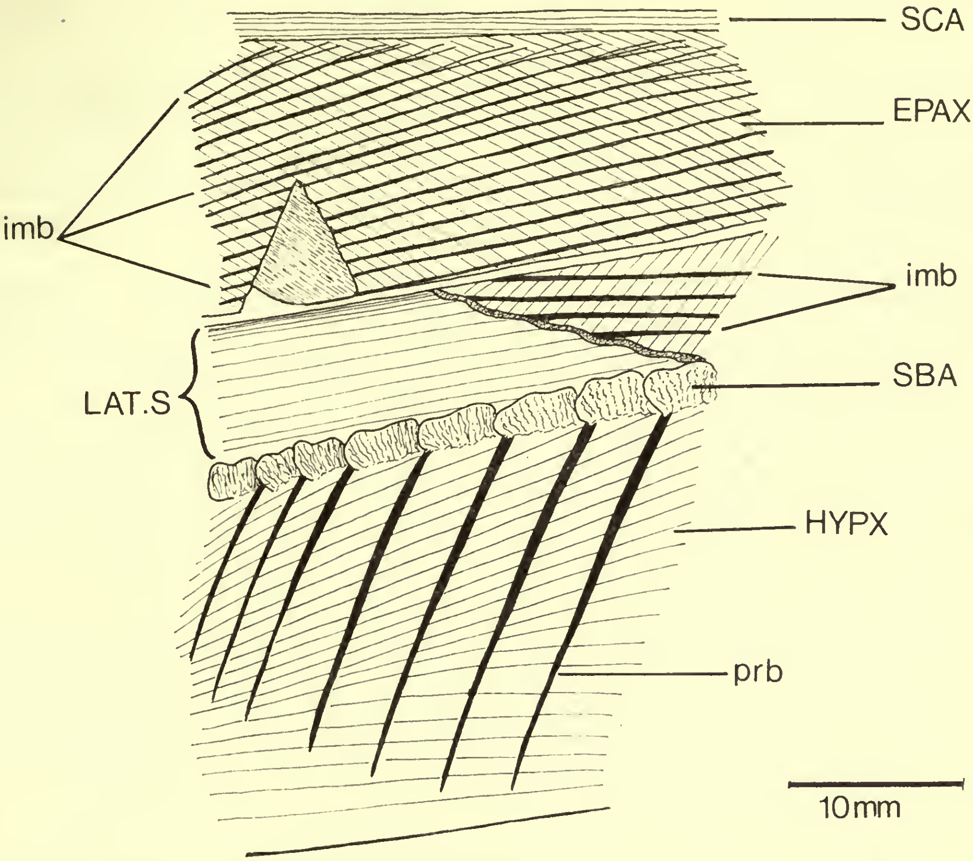


FIG. 14. *Rhaphiodon vulpinus*, section through the anterior body musculature showing the orientation of the intermuscular bones. Part of the *epaxialis* has been cut away to show the medial orientation of the fibres. All bones are shown in solid black.

In all three genera supraneural (predorsal) bones are numerous (*c.* 18–20) ; in *Rhaphiodon* they are reduced to slender rods.

The arrangement of the body musculature and intermuscular bony elements in *Rhaphiodon* obviously serves to counteract stresses from forces being applied anteriorly and along the dorsal surface of the body, such as might be produced by a dorso-posterior movement of the cranium.

The sabre-like canine teeth may serve as a trap to retain the prey in the mouth rather than as a means of impaling it. Removal of an impaled fish would be difficult and would require rapid movement of the jaws. It is likely that the fish relies on a suction method of feeding by rapidly activating the opercular mechanism (Alexander, 1967).

The narrow head affords a wide angle of vision which would certainly be stereoscopic anteriorly, ventrally and dorso-anteriorly.

Taxonomic Considerations

The status of the genus Roestes *Günther, 1864* (Figs 1D & 15)

The genus *Roestes* has been considered a member of the Characinae (*sensu* Eigenmann, 1909, 1910). Gery & Vu (1963) commented upon the similarities between this genus and *Hydrolycus*, remarking '. . . Il n'est pas impossible que *Roestes* fasse la jonction entre les Characinae et les Raphiodontinae'. Menezes (1974) revised the genus and included the following taxa in synonymy: *Lycodon, Gilbertella, Gilbertolus* and *Xiphocharax*.

Although Menezes presented an osteological description this was not complete, covering only the dermal cranial bones. From his study he concluded that *Roestes* was related to *Heterocharax* but that it did not belong to the same tribe as that genus, namely the Heterocharacini (see p. 234 for a discussion of this taxon).

My observations suggest that *Roestes* is not related to *Heterocharax* and furthermore that it is not even a member of the Characini but should be placed in the tribe Cynodontini on the basis of the following specialized characters shared with that group:

Adductor mandibulae section A_1 reduced (i.e. it does not extend along the ventral border of A_2 as in Characini);

Adductor mandibulae section A_2 is divided by the *levator arcus palatini* (never divided in the Characini);

Levator arcus palatini confined to the dorsal part of the hyomandibula (in the Characini the muscle extends ventrally along the anterior border of the bone);

Pectoral fin musculature is highly developed. The *abductor superficialis* is not separated from the *sternohyoideus* by the cleithrum as in the Characini; the accessory *abductor* muscle described in the Cynodontini (p. 221) is present.

Other, non-myological, characters are:

Teeth are arranged in a single series in both jaws (two rows present in either, or both, jaws in Characini, but with one exception, see p. 237);

The *coracoids* are extensively developed, extending far anteriorly and are joined medially along their entire midlines (in Characini the coracoids are only moderately developed and diverge posteriorly);

Pectoral fins are long, rays numbering I 17 (cf. I 12–15 in Characini);

Branchiostegal rays are five (four in Characini).

The skull displays no specialized characters which could be considered as essentially cynodontine or characinine. The dilatator fossa is moderately developed as in most Characini. A rhinosphenoid is present and the orbitosphenoid is widely separated from the parasphenoid; both features appear to be plesiomorph for the Characidae.

The hyomandibula is similar in form to that bone in the Characini.

Two other osteological characters which are noted in *Roestes* are the possession of well-developed intermuscular bones originating from the pterotic and a relatively high number of supraneural (predorsal) bones.

Cranially originating intermuscular bones appear to be a specialization amongst the characoids. Apart from the Cynodontini I have found them only in the Ctenoluciidae.

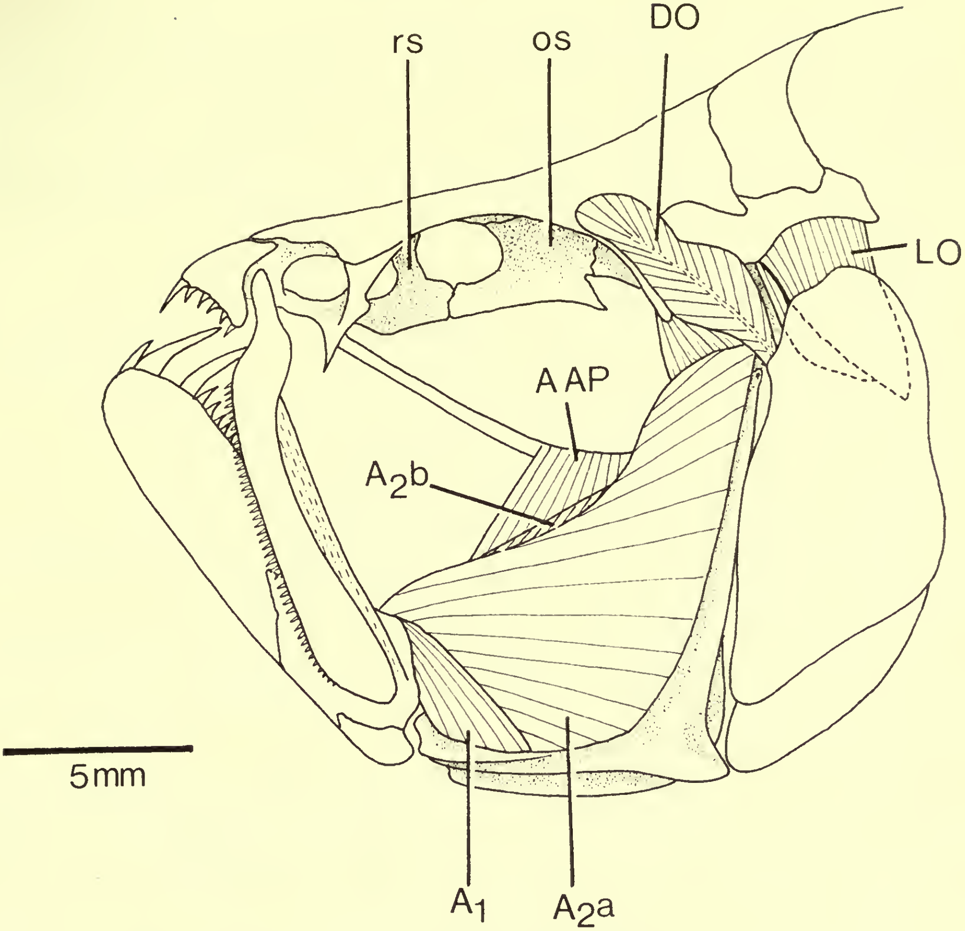


FIG. 15. *Roestes alatus*, superficial facial musculature, lateral view. The dashed lines on the operculum show the extent of the *levator* and *adductor operculi*.

The number of supraneurals varies considerably and appears in part to be correlated with the elongation of the body. In the Cynodontini they number 18–20, in the Characini never more than 5, in *Roestes* 8–9. Although in number this is closer to the Characini, *Roestes* is a relatively deep-bodied fish as compared with the characinine *Cynopotamus* and in this case the increased number does not seem to be a correlate of elongation (although it may reflect different stresses placed upon the dorsal surface of the body, see p. 225).

Intrarelationships of the Cynodontini

A combination of the following specialized characters is shared by all members of the Cynodontini :

Adductor mandibulae A_1 reduced to a small slip of muscle. A_2 is complexly pinnate with several origins ; it is divided by the *levator arcus palatini* ;

Dilatator operculi origin from both the dorsal and ventral surfaces of the frontals (except in *Roestes* where origin is entirely from the dorsal surface) ;

Levator operculi origin in part from the tendon of the *lateralis superficialis* and in part from the supracleithrum ;

Sternohyoideus dorsally divided ;

Pectoral fin musculature extensively developed, the *abductor superficialis* being virtually continuous with the *sternohyoideus* (i.e. not separated by the cleithrum), and an accessory *abductor* muscle present ;

First obliqui ventrales divided ;

Non-myological specializations are :

Branchiostegal rays number five, the first three spathiform, the two posterior ones acinaciform ;

Hyomandibular bone modified (except in *Roestes*) ;

Coracoids extensive, closely applied or fused ;

Sphenotic process well developed, sometimes laterally extended ;

Intermuscular bones originating from the posterior of the cranium.

Although none of the non-myological characters (with the exception perhaps of the modified hyomandibular bones) is confined to the Cynodontini, no other characoid is known to possess more than three of these in combination.

It would seem that there are two groups of species constituting the Cynodontini.

1. *Rhaphiodon* and *Cynodon* are characterized by having depressed crania, stout horizontal parasphenoids articulating with the orbitosphenoids and prominent laterally directed sphenotic processes.

It is difficult to say which of these two genera is more highly specialized. Nelson (1949) showed that the swimbladder in *Rhaphiodon* was of a complex structure possessing numerous appendices, some of which penetrate the body wall (SBA, Fig. 14). In *Cynodon* (and other cynodontine genera) the swimbladder does not appear to be specialized in this way. It is shorter than that found in *Rhaphiodon*, extending to just past the origin of the anal fin, and there are no appendices in contact with the body wall (although in *Roestes* the *tunica externa* is closely applied to the body wall).

In *Cynodon* the rhinosphenoid is absent, a feature perhaps correlated with the depression and elongation of the skull.

2. *Hydrolycus* and *Roestes* are characterized by a rather more vaulted cranium, a curved parasphenoid well separated from the orbitosphenoid, and narrow, posteriorly directed sphenotic processes.

Roestes differs from all other cynodontine genera in lacking the highly specialized development of the *adductor mandibulae* A_2 and *dilatator operculi*. Also absent is the modified hyomandibula.

The genus *Roestes* appears to occupy something of an intermediate position between the Characini and Cynodontini and is possibly the most primitive extant representative of the tribe.

The possible phyletic relationships of the tribe Cynodontini are shown in Fig. 21.

Tribe **CHARACINI** Fowler, 1958

Characidi Fowler, 1958
Characinae Eigenmann, 1909

The Characinae was erected by Eigenmann (1909; genera enumerated, 1910) to contain the following genera: *Charax* Scopoli, *Roestes* Günther, *Gilbertolus* Eig., *Roeboides* Günther, *Bramocharax* Gill, *Eucynopotamus* Fowler, *Evermannolus* Eig.,

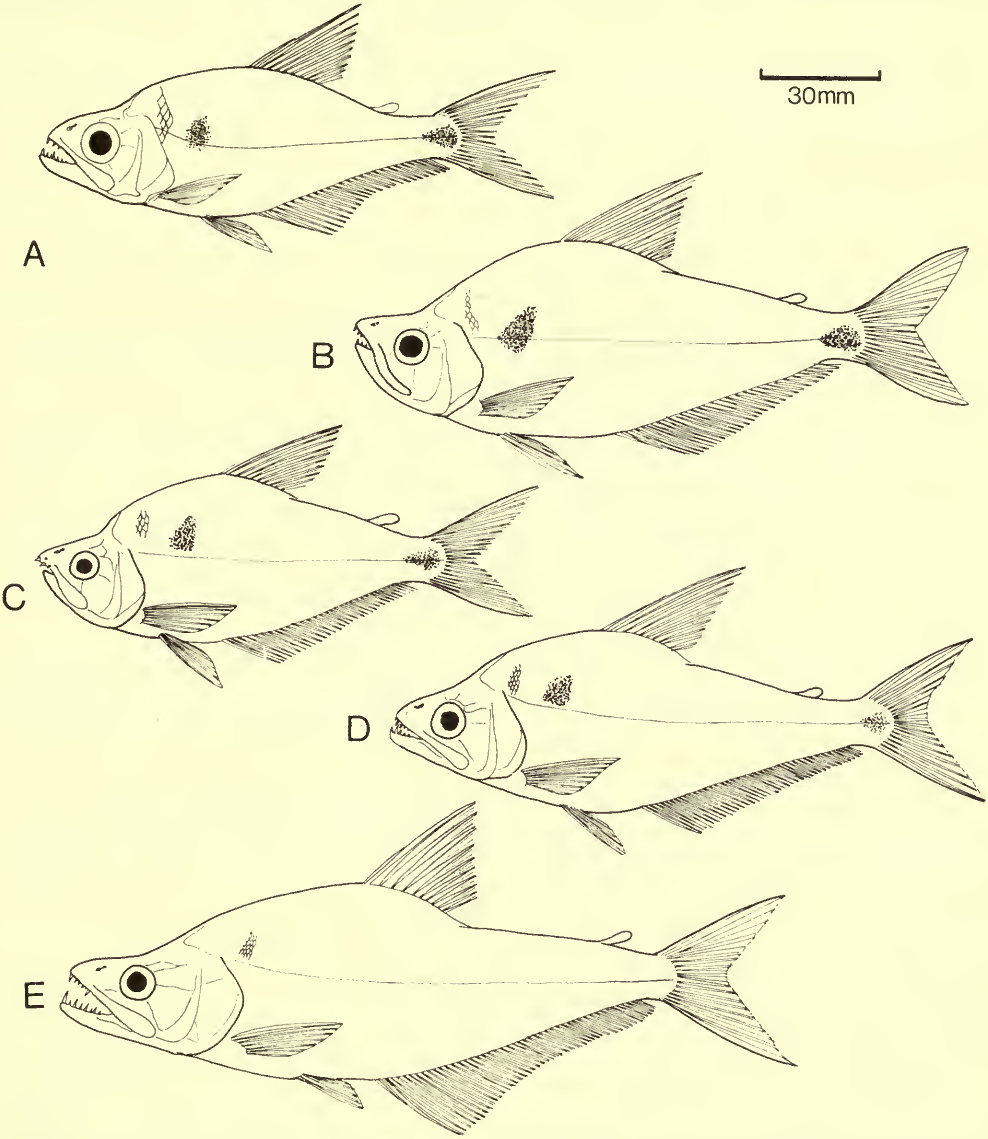


Fig. 16. Outline drawings of (A) *Acanthocharax microlepis*, (B) *Charax gibbosus*, (C) *Roeboides dayi*, (D) *Cynopotamus* (*Hybocharax*) *magdalenae* and (E) *Cynopotamus* (*Cynopotamus*) *argenteus*. All drawn to scale.

Asiphonichthys Cope, *Salminus* Agassiz, *Catabasis* Eig. & Norris and *Exodon* Müller & Troschel (*Cynopotamus* Val. was considered a synonym of *Charax*).

Later, Eigenmann (1912a) included *Acanthocharax* and *Heterocharax*. Subsequent authors have added other genera, including *Cyrtocharax* Fowler, 1906; *Genycharax* Eig., 1912; *Gnathocharax* Fowler, 1913; *Lonchogenys* Myers, 1927; *Moralesia* Fowler, 1943; *Roeboexodon* Gery, 1959; and *Hoplocharax* Gery, 1966. This list does not include those genera considered to be synonyms of any of the above taxa.

The inclusion of these genera in the tribe on the basis of shared specialized myological characters is discussed on pp. 233–238. *Charax gibbosus* forms the basis for the following description of the cranial musculature.

Description of the Cranial Musculature of *Charax gibbosus* (Linn.)

(Fig. 16B)

Facial musculature (Fig. 17)

Adductor mandibulae section A_1. This is a small element lying at an angle of 45°. It originates posteriorly from the preoperculum and the ventral edge of the quadrate to insert along the dorsal edge of the angulo-articular.

Extending from this insertion is the extensive connective tissue band which joins the maxillary to the lower jaw. As in the Cynodontini the '*ligamentum primordiale*' is in fact a thickening of the folded tissue that forms the floor of the orbital cavity. Posteriorly, however, the tissue does become differentiated into a 'ligament' which passes laterally to A_1 and is attached to the outer face of the angulo-articular. (This condition is found throughout the Characini, the folded skin enabling the maxillary to move well forward when the mouth opens.)

Section A_2 originates dorsally and medially from the hyomandibula and posteriorly from the preoperculum. Ventrally a strong tendon runs from the quadrato-preopercular region to join the aponeurosis of the *adductor mandibulae* at the jaw articulation.

The aponeurotic sheet is a small triangular area, the ventrally directed apex of which gives rise to the stout tendon that forms the posterior border of A_w.

Section A_w fills the coronomecklian cavity. It is a bipinnate muscle, the midline raphe stretching to a point halfway along its length.

Levator arcus palatini. This muscle extends from the ventral surface of the sphenotic process to insert upon the hyomandibula. In some specimens, fibres extend also from the ventral surface of the frontal.

Adductor arcus palatini. This is a short element confined to the posterior section of the parasphenoid. Insertion is upon the metapterygoid and hyomandibula.

Dilatator operculi. This muscle takes its origin from the fossa formed by the frontal and sphenotic, and also from the lateral border of the pterotic; dorsally the pterotic border (at the anterior termination of the pterotic canal) forms a strong indentation in the muscle. Insertion is via a short thick tendon on to the medial face of the anterior opercular process.

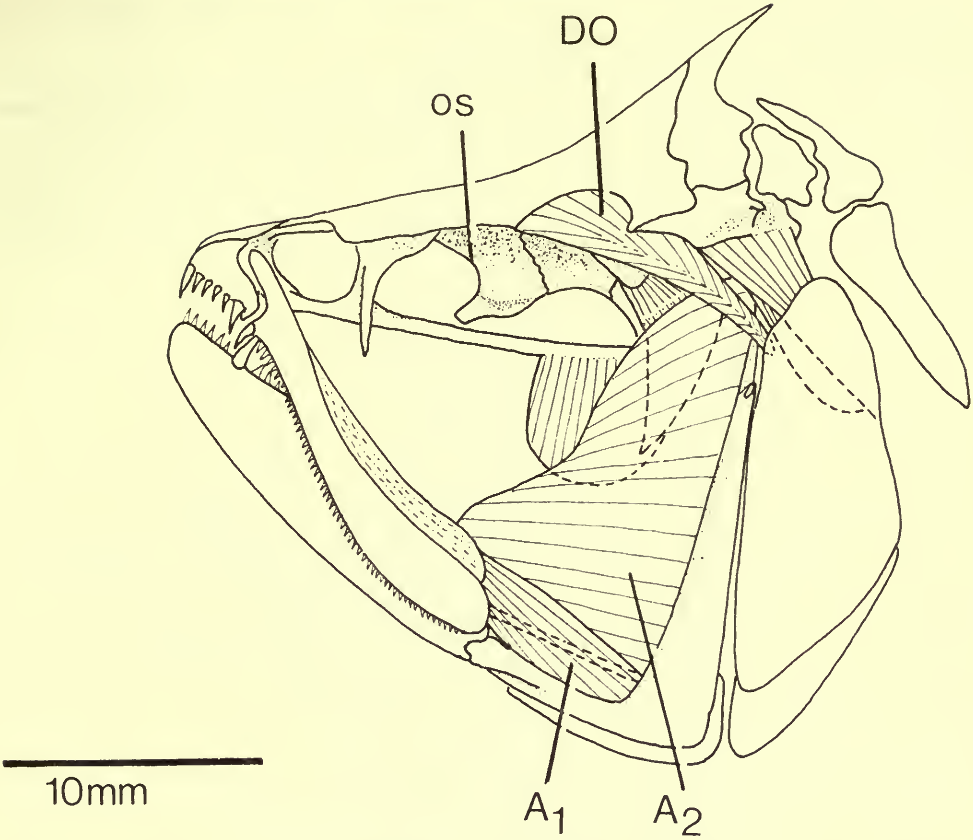


FIG. 17. *Charax gibbosus,* superficial facial musculature, lateral view. The dashed lines indicate the borders of the *adductor arcus palatini, levator arcus palatini, levator* and *adductor operculi.* The dashed lines across *adductor mandibulae* A_1 show the position of the underlying tendon which is the ventral border of A_2.

Levator and *adductor operculi.* The *levator* is a triangular muscle, whose base extends along the lateral border of the pterotic, and the apex inserts along the posterior medial surface of the operculum. The *adductor* stems from a shallow subtemporal fossa and inserts anteriorly to the *levator.*

Hyoid musculature (Fig. 18)

Protractor hyoidei. This extends from the second and third branchiostegal rays to run over the first ray and the ceratohyal. The elements of each side unite into a single short medial section which inserts dorsally and ventrally to the *intermandibularis.*

Hyohyoidei. These are weakly developed (see p. 216). The 'abductores' sections run from the first branchiostegal rays to the hypohyals. As in the Cynodontini, the hypohyals are covered by a connective tissue fascia which extends dorsally to cover the basihyal.

The 'adductores' parts of the muscle are extremely thin, only a single layer of fibres running between the branchiostegal rays.

Sternohyoideus (SH, SHD, Fig. 18). This is a deep muscle taking its origin entirely from the cleithrum and inserting along the lateral face of the compressed urohyal. Dorso-laterally the muscle is divided (as in the Cynodontini). The insertion of the dorsal division is via a long tendon on to the third hypobranchial. Prior to insertion the tendon is joined by its fellow from the opposite side, the two becoming firmly united along the midline before diverging to their respective insertions.

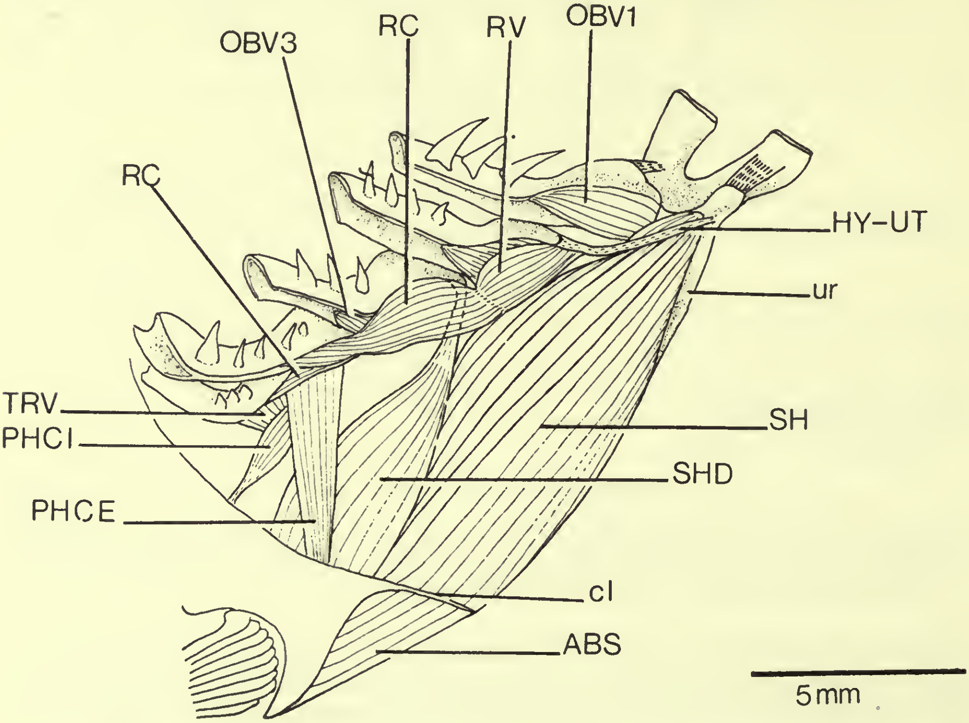


FIG. 18. *Charax gibbosus*, ventral branchial arch and hyoid musculature, lateral view.

A similar tendon is present in the Cynodontini (Fig. 10) although it is not as strongly developed. Nor, in that tribe, does it serve as the insertion tendon for the dorsal division of the *sternohyoideus*. A similar tendon is present in other characoids. I have observed it in *Brycon falcatus*, *Hoplias malabaricus* and *Acestrorhynchus* species.

Dietz (1914) refers to a similar tendon being present in *Gobius*. (See also Winterbottom, 1974 concerning the *sternobranchialis* ; also fig. 27 in that work illustrating a ventral tendon in *Elops*.)

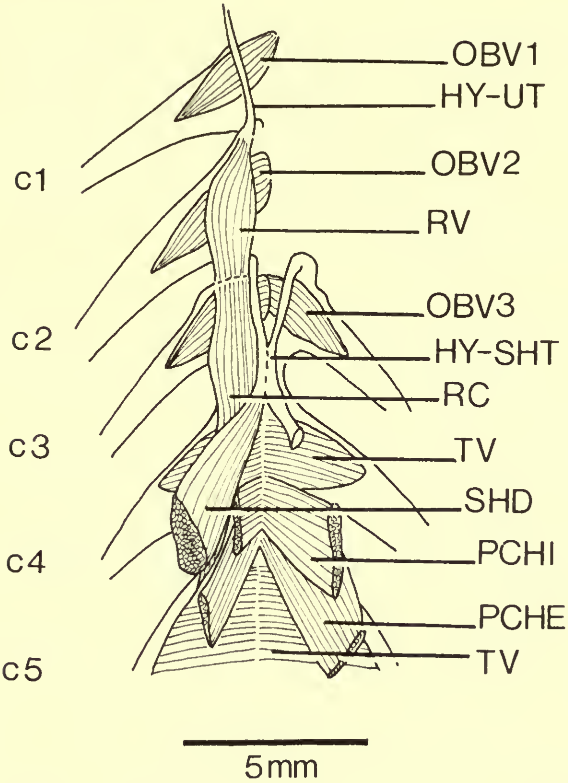


FIG. 19. *Charax gibbosus*, ventral branchial arch musculature, ventral view. Some of the elements have been cut through or removed.

Muscles of the branchial arches (Figs 18 & 19)

The arrangement is similar to that described for the Cynodontini.

Rectus ventralis (RV). This is bordered anteriorly by a long tendon which runs from the second hypobranchial to insert upon the urohyal (HY-UT).

Rectus communis (RC). This is very short and thick, extending from the third hypobranchial to insert on the fourth and fifth ceratobranchials.

Obliqui ventrales (OBV 1–3). These are well developed. OBV 1 shows something of a medial division but is not completely divided as in the Cynodontini.

Taxonomic Considerations

The genera of the Characini

There is much confusion concerning the taxonomy of the genera and species assigned to the Characini (Characinae *sensu* Eigenmann ; see Schultz, 1950 ; Gery, 1972a ; Gery & Vu, 1963). The assortment of genera listed above (p. 229) does not, in my opinion, constitute a monophyletic assemblage and on these grounds some genera should be excluded from the Characini as here defined. A review of these genera shows the current status of the taxa to be as follows.

Roestes. Elsewhere in this paper (p. 226) reasons have been given for including this genus in the Cynodontini.

Gilbertolus. This is a synonym of *Roestes* (see Menezes, 1974).

Bramocharax. This is a tetragonopterine, possibly related to *Astyanax.* The species have been described and the genus discussed by Rosen (1970, 1972).

Eucynopotamus. This has been considered a subgenus of *Charax* by Gery & Vu (1963). Due to lack of material I have been unable to assess the validity of 'subgenera' within the *Charax* group.

Evermannolus. This is a synonym of *Eucynopotamus* (see Schultz, 1950 ; Gery & Vu, 1963).

Salminus. This genus is certainly not related to any of the genera here included in the Characini. Myologically it is specialized (pers. obs.) and would appear to be related to the Bryconini–Tetragonopterini lineage (see also remarks on interrelationships by Roberts, 1969 : 435–7).

Catabasis. This genus is known only from the holotype of *C. acuminatus* and is considered by Roberts (1969 : 438) to be '. . . a distinct genus of Characidae'. Its status cannot be assessed until further material comes to hand.

Exodon. Superficially this genus resembles *Roeboides,* possessing external teeth along the upper jaw. However, the cranial musculature is that of a tetragonopterine or bryconine fish (pers. obs.).

Gery (1959) considered that *Exodon* together with *Roeboexodon* constitute part of a lineage, including *Holobrycon* (*Brycon*), which is related to *Roeboides.* Purely on myological grounds I do not believe that *Exodon* is related to *Roeboides* and I can find no evidence to suggest that it belongs to the Characini. Its true relationships may become apparent after detailed osteological study.

Heterocharax, Lonchogenys and *Hoplocharax.* Gery (1966) established a 'subtribe', the Heterocharacini, to contain these three monotypic genera.

Apart from the conical dentition, *Heterocharax macrolepis* shares none of the specialized features associated with the Characini. The cranial musculature is typically that of a tetragonopterine (i.e. large *adductor mandibulae* A_1 indistinctly separated from A_2 posteriorly ; *dilatator operculi* restricted to a small, laterally situated sphenotic fossa ; *sternohyoideus* undivided and originating from the cleithrum). The coracoids are small and widely divergent posteriorly. The orbitosphenoid is reduced ; a rhinosphenoid is present.

I have been unable to examine specimens of *Lonchogenys* or *Hoplocharax.*

Gery (1966) considered that this subtribe was '. . . still rather close to the generalized tetragonopterine type'. I would agree with this statement and for the present the phyletic position of the 'subtribe' Heterocharacini must remain uncertain but it can be excluded from the Characini.

Gnathocharax. Eigenmann (1916) suggested that this genus was closely related to *Roestes* (cited as *Gilbertolus* in that paper). This view was endorsed by Böhlke (1955) who stated : 'The characteristics shared by the two genera are overwhelming and their common ancestry seems certain.' In its general morphology *Gnathocharax* certainly does resemble *Roestes,* particularly in possessing elongate pectoral fins. It shares also the expanded coracoids which are closely applied along the midline. However, the lower jaw is shallow, and the dentition is of a rather different pattern (features shared with *Heterocharax*). Again, the cranial musculature is of the tetragonopterine type and the hyoid muscles show none of the specializations of the Characini.

I find this genus something of a problem: certainly there are no myological features that would place it unequivocally in the Characini or the Cynodontini. As far as I can see osteologically it greatly resembles *Heterocharax*, apart from the development of the coracoids (which is probably a parallel of this character in *Roestes*). For the moment I would suggest that *Gnathocharax* be included within the 'Heterocharacini'.

Genycharax. This monotypic genus Eigenmann (1912b) related to '. . . the Tetragonopterinae on the one hand and to *Exodon* on the other'.

Miles (1947) placed the genus in the Characinae (Characini in this paper).

The teeth are conical, those forming the outer row on the premaxilla (numbering 12–16) are directed forwards, those on the inner row are curved inwardly, as are those in the lower jaw.

The only specimen I have been able to examine is badly preserved and I am unable to determine whether the *adductor mandibulae* A_1 is reduced to the same degree as in the Characini (see below). There is, however, a dorsal division of the *sternohyoideus* which is a specialization shared with that tribe. The *dilatator operculi* occupies a small fossa.

I have refrained from assigning this genus to the Characini until more material is available.

Genycharax tarpon appears to be confined to the Cauca river of Colombia.

The remaining genera to be considered from those listed on p. 230 are *Charax*, *Roeboides*, *Acanthocharax*, *Cyrtocharax*, *Cynopotamus*, *Moralesia* and *Asiphonichthys*.

By virtue of the following shared myological specializations these taxa are considered to constitute the tribe Characini.

The *adductor mandibulae* section A_1 is reduced and is completely separated from A_2, extending along the entire ventral border of that element. In Tetragonopterini and Bryconini it is large and posteriorly the fibres are confluent with those of A_2.

The *levator arcus palatini* sometimes originates from the ventral surface of the frontal. This condition has not been found in Tetragonopterini or Bryconini.

The *dilatator operculi* is long and sometimes extends far on to the dorsal cranial surface. In Tetragonopterini this muscle is always confined to a small laterally placed fronto-sphenotic fossa. It may, however, be found to extend well forward in some species currently placed in the genus *Brycon* (pers. obs.).

A dorsal division of the *sternohyoideus* is present and inserts, via a tendon, on the leading edge of the third hypobranchial. Apart from the Cynodontini, no such division of this muscle has so far been found in any other group of characoids.

Charax and *Roeboides*. Myologically, *Charax* most closely resembles *Roeboides* (cf. Figs 17 & 20B). In both genera the *dilatatores operculorum* run from a shallow fossa (which is strongly indented by the anterior border of the pterotic canal and by the parietal) formed by the frontal and sphenotic. In *Roeboides* (*guatemalensis*, *prognathus* and *myersii*), however, the sphenotic extends further laterally.

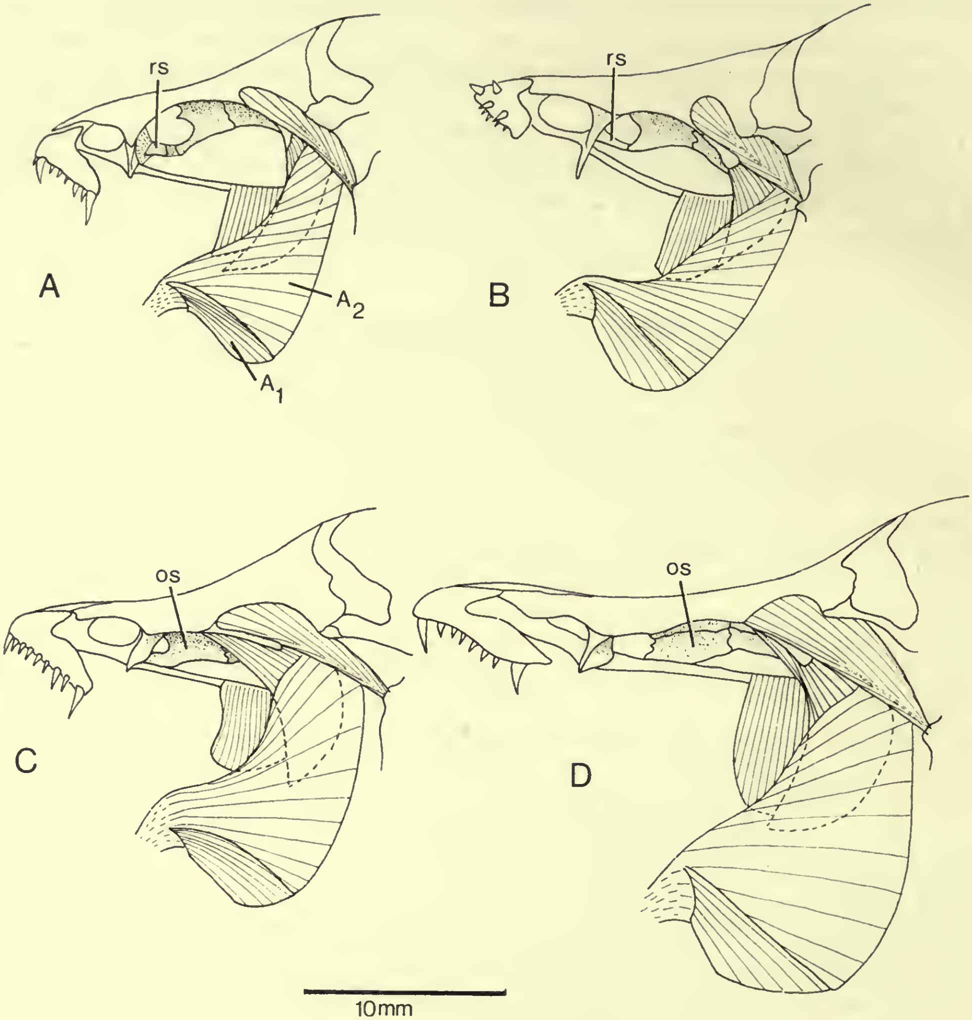


FIG. 20. Superficial facial musculature of (A) *Acanthocharax microlepis*, (B) *Roeboides prognathus*, (C) *Cynopotamus* (*Hybocharax*) *magdalenae* and (D) *Cynopotamus* (*Cynopotamus*) *argenteus*. The dashed lines indicate the borders of the *levatores* and *adductores arcus palatini*.

The *levator arcus palatini* is developed to about the same degree in both genera.

The tendon running from the dorsal division of the *sternohyoideus* to the third hypobranchial is strongly developed.

At this point some mention should be made of certain osteological features which to my knowledge have not been recorded for these genera.

In *Charax* the rhinosphenoid is absent. The orbitosphenoid is in close contact with the parasphenoid. In a series of eleven specimens of *Charax gibbosus* ranging in size from 103 to 70 mm S.L. the degree of contact between the orbitosphenoid and parasphenoid varied, from being narrowly separated to completely united; the degree of separation does not appear to depend on the size of the specimen. This feature (which is also seen in *Cynopotamus*) conflicts with one of the criteria used by Weitzman (1962 : 48) in defining the subfamily Characinae, namely, that the orbitosphenoid is not directly articulated with the parasphenoid. I would consider that such a feature is a specialization correlated with elongation and depression of the skull (a similar situation occurs in *Cynodon* where the orbitosphenoid and parasphenoid are in contact and the rhinosphenoid is absent, see p. 228).

In *Roeboides prognathus* (Fig. 20B) and *R. guatemalensis* the rhinosphenoid is well developed and extends anteriorly of the orbitosphenoid. In *Roeboides myersii*, however, it appears to be absent.

Moralesia. I have been unable to examine any specimens of species belonging to this genus. This taxon has been considered by Böhlke (1958 : 70) to be a distinct genus related to *Charax*. Gery & Vu (1963) consider it a subgenus. Whatever the rank accorded to this taxon, it does appear to belong to the Characini.

Cynopotamus (Figs 16D & E and 20C & D). Gery & Vu (1963) divided this genus into several subgenera. I have examined species representing all these taxa, namely, *C.* (*Cynopotamus*) *argenteus*, *C.* (*Cynopotamus*) *limaesquamis*, *C.* (*Hybocharax*) *magdalenae* and *C.* (*Acestrocephalus*) *goeldii*.

All these species display a long *dilatator operculi*, the fibres of which are shallowly bipinnate. In *C.* (*Cynopotamus*) *argenteus* some ventral fibres of this muscle take their origin from the sphenotic process (a condition also encountered in *Hydrolycus* of the Cynodontini, see p. 215). The form of the dilatator fossa differs somewhat between the subgenera. In *C.* (*Hybocharax*) *magdalenae* the shelf formed by the frontal and sphenotic is posteriorly directed, whereas in *C.* (*Cynopotamus*) *argenteus* and *C.* (*Acestrocephalus*) *goeldii* it is somewhat laterally extended (cf. Figs 20C & D).

In all species examined the dorsal division of the *sternohyoideus* is well differentiated and extends via a long thick tendon to its insertion on the third hypobranchial.

The branchial muscles show something of a modification from those in *Charax* and *Roeboides*. The *obliqui ventrales* are thin and compressed as is the *rectus ventralis* and *rectus communis*. The division between these two elements is not effected by the interface of connective tissue, and the ventral fibres of the *rectus communis* appear to be continuous with those of the *rectus ventralis*.

The median ethmoid of *Cynopotamus* (*Cynopotamus*) *argenteus* is extended and the skull is greatly depressed anteriorly.

Cyrtocharax. This is a synonym of *Cynopotamus* (see Gery & Vu, 1963).

Asiphonichthys. This genus differs from all others here placed in the Characini in possessing a single row of teeth in both jaws. I have only a single specimen of *A. stenopterus* available, and unfortunately its mouth has been damaged. However, the larger canines in the upper and lower jaws appear to be placed slightly medial to the other close-set teeth, as indeed do some of the more posterior teeth.

As far as I can see, there are no other characters, osteological or myological, which would suggest that this genus is other than a member of the Characini.

Acanthocharax (Figs 16B & 20A). This monotypic genus exhibits a more 'generalized' appearance than do any of the other taxa included in this group. The jaws are not so obliquely aligned, the mandibular teeth are numerous and slightly curved ; the body shape does not display a marked gibbosity and there is no ventral keel.

The principal myological differences are again seen in the form of the *dilatator operculi* and its accommodating fossa. The muscle is long, almost unipinnate, and the shelf on the sphenotic is posteriorly directed.

The *levator arcus palatini* is reduced antero-posteriorly and its crescentic lower border extends further ventrally on to the face of the hyomandibula than it does in the other genera examined.

The dorsal division of the *sternohyoideus* is present, inserting through short tendons on to the third hypobranchial.

The parasphenoid is somewhat curved (as in most tetragonopterines and bryconines) and is widely separated from the orbitosphenoid. The rhinosphenoid is well developed and extends anteriorly from the orbitosphenoid, to which it is attached by a band of ligamentous tissue.

Interrelationships of the Characini

Gery (1959) sought to establish a relationship between the characinine *Cyrtocharax* (= *Cynopotamus*) and *Acestrorhynchus* (Acestrorhynchinae). I can find little to substantiate this view. The conical dentition is probably a primitive character for these genera, and the predatory facies is most likely a case of parallelism (see p. 240). However, there are no shared characters which could be termed specialized. In both myological and osteological features *Acestrorhynchus* differs considerably from any member of the Characini. Work is in preparation to establish the nature of its relationship with other characoid taxa.

Of the groups of species recognized as subgenera by Gery & Vu (1963), *Cynopotamus* and *Acestrocephalus* seem to be the most extreme and represent the specialized predator lineage of the tribe, which has possibly been derived from the basal *Charax–Roeboides* ancestral group.

Just how closely related are *Charax* and *Roeboides* is difficult to say. They certainly resemble each other in their muscle morphology, but these resemblances are plesiomorphic for the Characinae. No comparative osteological studies of these genera have been made and those undertaken in the course of this study have been rather limited. For the moment I would suggest that *Charax* and *Roeboides* are more closely related than are either to any other taxon within the Characini.

I am treating *Acanthocharax* as the representative of the plesiomorph lineage of this group. This is mainly on the basis of the 'generalized tetragonopterine' skull and relatively unspecialized dentition.

Because of lack of material I have been unable to place the genera *Moralesia* and *Asiphonichthys*. *Moralesia* would certainly seem to be closely related to *Charax* (see p. 237) ; the relationships of *Asiphonichthys*, however, are rather more obscure. It is the only genus of the Characini to possess a single row of teeth in both jaws (p. 237) ; whether this is a primitive or a derived condition for the Characinae is

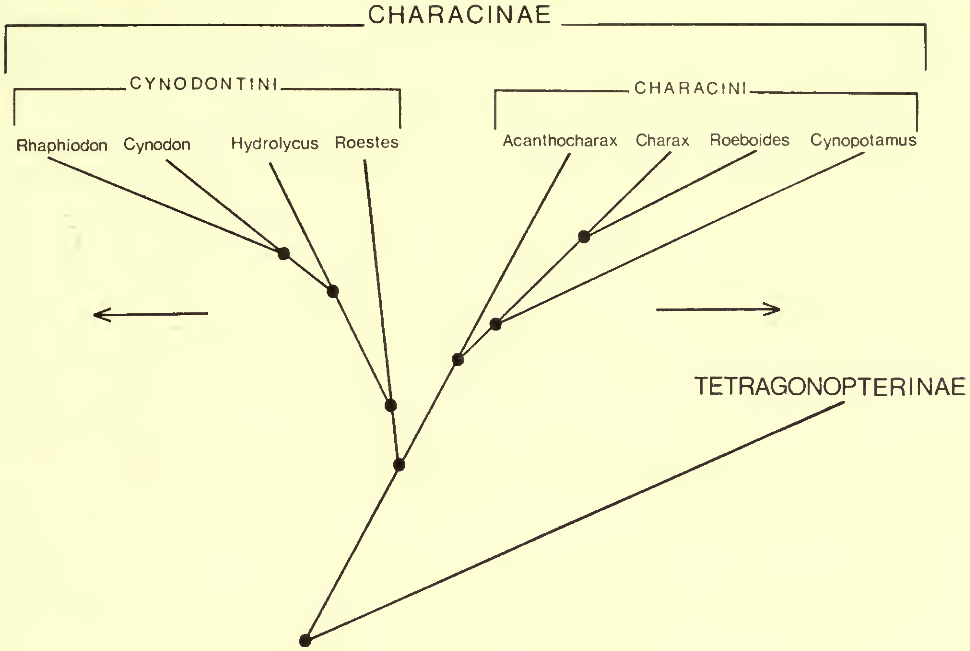


FIG. 21. Cladogram of the Characinae. The arrows indicate the trends toward elongation of the body, increase in the number of body scales, lengthening of the anal fin and development of specialized dentition. The positions of the genera *Asiphonichthys* and *Moralesia* are not indicated (see pp. 237–238).

not known at present. *Asiphonichthys* is probably a derivative from the *Charax–Roeboides* lineage.

The specialized myological features found in all Characini and shared with all Cynodontini are the reduced *adductor mandibulae* section A_1 and the divided *sternohyoideus*. These are not, as far as I know, found in other characoid taxa.

I would consider the Cynodontini and Characini to be sister tribes, together forming the subfamily Characinae. The Characinae in turn is the sister group of the Tetragonopterinae (= Characinae of Weitzman, 1962).

Remarks on the genus Agoniates *Müller & Troschel, 1845*

The genus *Agoniates* presents something of a problem. Regrettably I have been unable to examine any specimens and thus am unable to comment on myological features or to make any constructive observations except to consider the possibility of its relationship with the Cynodontini. The pattern of dentition, the number of branchiostegal rays (5 according to Gery, 1963), and the length of the pectoral fins may be shared specializations.

Gery (1963) considered, on the basis of cranial and scale morphology, that *Agoniates* is not related to the cynodontine fishes but is more closely related to the Bryconini.

DISCUSSION

The species comprising the tribe Cynodontini are seemingly adapted for a specialized predatory existence. Unfortunately, due to a complete lack of biological and ecological information, the exact nature of this mode of life is unknown.

Of course, other characoids have adopted the predatory roles but these have assumed the familiar 'pike-like' facies. Examples are to be found in the Hepsetidae, Ctenoluciidae and Acestrorynchinae. Unpublished myological studies of these taxa have shown that they can be clearly separated from other characoids on the basis of at least one shared skeleto-myological feature, namely the morphology of the *dilatator operculi* and its accommodating fossa. In all (apart from *Hepsetus*) the muscle originates from the ventral surface of the frontal and is directed through a tunnel, the roof of which is formed by the frontal and the floor by the autosphenotic, the bones being sutured along their lateral margins (noted in *Erythrinus* by Weitzman, 1964; in *Hoplias* by Alexander, 1964; in *Acestrorhynchus*, *Ctenolucius* and *Boulengerella* by Roberts, 1969).

Another characteristic of these pike-characoids is the relatively flat skull in which the long sphenotico-pterotic region provides an increase in the area of origin for the *adductor mandibulae* muscles. Also, as Alexander (1964) has pointed out in discussing *Hoplias*, these fish benefit from possessing long *dilatatores operculorum* muscles, since such muscles are probably used to boost the water currents entering the mouth, thereby assisting in the capture of prey.

The *dilatator operculi* is basically a parallel fibred muscle and in order for it to achieve the necessary force either it can operate over an increased distance to allow for the necessary shortening of the fibres, or it can increase the area of its origin and become pinnate, thus obtaining the same mechanical advantage.

Just which form the muscle takes will depend upon other demands imposed upon the cranium. Thus, in the pike-characoids, which present a 'streamlined' profile, the muscle is concealed below the cranial roof. Here, however, the area of origin is too restricted to allow for a well-developed pinnate form of the muscle, and reliance is placed on utilizing the orbital-opercular distance. In those characoids where the skull is vaulted the *dilatator operculi* can extend to the dorsal surface of the cranium to run obliquely downwards. Here the area of origin is greatly expanded, as in the Cynodontini, and the muscle is distinctly pinnate. It may be mentioned here that the characoid *Anodus* (Hemiodontidae; see Roberts, 1975) has a very large operculum. This fish is not a predator but seems to feed on plankton and, possibly, detrital material. Here, again, the *dilatator operculi* has become enormously developed and extends over the entire frontal region.

In the pike-characoids an increased area of origin for the *adductor mandibulae* is provided by the long sphenotico-pterotic border, with a consequent increase in the area of the hyomandibula. The advanced species of the Cynodontini have evolved a predatory facies not by elongation of the ethmoid or the postorbital skull region as in the pike-characoids, but by a reorientation of the jaw suspensorium. This is achieved by the quadrate and metapterygoid shifting into an almost perpendicular position, by correlated modifications to the hyomandibula (see remarks by Nelson, 1949: 505), by lengthening of the maxilla and the lower jaw, and by expansion of the dilatator fossa on to the dorsal surface of the cranium. It is interesting to note here the different reorganization involved in achieving the same 'solution' in the cyprinid *Macrochirichthys* (p. 245), where a reorientation of the muscles rather than of the bony supports seems to have occurred.

The lineage which gave rise to the Cynodontini would appear to have been an early off-shoot from the basal group which also gave rise to the Tetragonopterinae and related taxa. Somewhat parallel trends are seen in both the Cynodontini and Characini, producing specialists with elongate bodies, more scales, large mouths, raptorial dentition and a consequent parallel development of the cranial musculature. However, such an extreme form as *Rhaphiodon* has not arisen in the Characini.

The morphology of the cynodontine species suggests an existence at, or close to, the surface of the water, whereas the pike-characoids tend to occupy the mid-water levels. Thus, there is unlikely to be direct competition between these two groups.

ACKNOWLEDGEMENTS

I am indebted to Dr P. H. Greenwood not only for his valuable guidance, advice and criticism throughout the course of this study, but particularly for his constant encouragement and stimulation.

My grateful thanks go to Dr K. E. Banister for his assistance on osteological problems, to Mr J. Chambers for producing such fine alizarin preparations, to Mrs Margaret Clarke for drawing my attention to various cyprinoids and to Dr P. J. P. Whitehead for his advice on nomenclatural matters and for his criticism of the manuscript.

Finally, and not least, go my thanks to Dr R. H. Lowe-McConnell for providing information on living characoids and for sparing so much time in discussing them.

APPENDIX

Observations on the cranial anatomy of the cyprinid fish *Macrochirichthys macrochir* (Val.)

(Figs 22–24)

A remarkable example of parallelism is seen when the cynodontine characoid *Rhaphiodon vulpinus* is compared with the cyprinid *Macrochirichthys macrochir*, a species recorded from Thailand, Java, Sumatra, Borneo and Malaysia (Smith, 1945) and from China (Wu, 1964). (The term 'parallelism' rather than 'convergence' is used here because it is assumed that the cyprinoids and characoids share a common (albeit a relatively remote) ancestry, and thus have presumably inherited a common genetic capacity that will respond by producing similar adaptations to similar environmental pressures.)

Both *Rhaphiodon* and *Macrochirichthys* exhibit the same extreme elongation of body, inclination of the jaw, markedly elongate pectoral fins and position of median fins (cf. Figs 22 & 1C). However, the arrangement of the cranial muscles in *Macrochirichthys* differs quite considerably from those in *Rhaphiodon* (Figs 23 & 24).

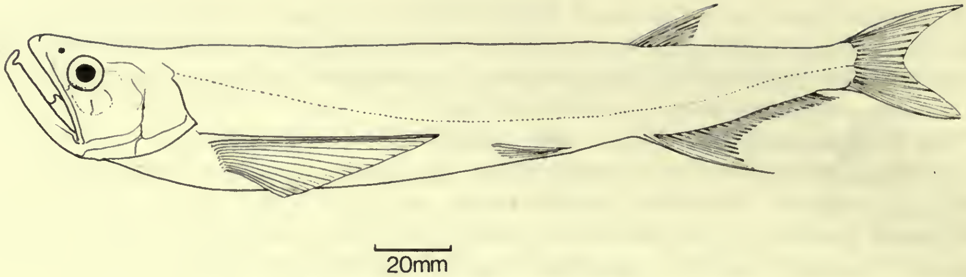


FIG. 22. *Macrochirichthys macrochir*, outline drawing.

The frontals provide attachment for epaxial musculature, which extends anteriorly as far as the ethmoid.

The *dilatator operculi*, which is such a prominent feature in *Rhaphiodon*, is reduced to a small element running from the sphenotic and pterotic to the edge of the operculum.

The *levator operculi* is large ; it originates along the entire pterotic border and runs along the medial surface of the operculum.

The *adductor operculi* joins the *levator* anteriorly (I am unable to determine the precise origin of the *adductor* from the single specimen at hand).

The facial muscles also show quite a departure from the arrangement in the characoid.

The external cheek muscle, the *adductor mandibulae* section A_1, originates from the quadrate and preoperculum and from the mass of the underlying section A_2. Insertion is along the lateral dorso-posterior border of the wide maxilla (both maxillary and premaxillary bones are firmly sutured for their entire lengths, thus together forming a thick, heavy upper jaw). This development of the insertion of A_1 suggests a more active role for the upper jaw than in *Rhaphiodon*.

Adductor mandibulae section A_2 originates from the hyomandibula to insert upon a wide aponeurosis. Medially there lies another element which also takes its origin from the hyomandibula. I cannot be certain whether this is A_2a or A_3 (following the nomenclature of Takahasi, 1925, this would be A_3). The muscle is greatly thickened antero-ventrally, its fibres being folded over and running almost perpendicularly to join those of the outer element.

The *levator arcus palatini* (Fig. 24) is a complex muscle originating both from the ventral surfaces of the frontals and from the sphenotic. An outer bundle of fibres is somewhat separated from the main element and inserts tendinously upon a small, anteriorly directed process of the hyomandibula. Posteriorly the main part of the muscle inserts in a hyomandibular fossa.

The *adductor arcus palatini* (AAP, Fig. 24) is a small muscle having a very narrow origin posteriorly on the parasphenoid ; it inserts ventrally on the metapterygoid. A thin fibrous sheet of connective tissue (TCT, Fig. 23) extends the length of the parasphenoid, and is closely applied to the metapterygoid laterally. The fibres within this sheet are orientated postero-ventrally at an angle of *c.* 30° to the horizontal.

The pectoral fin musculature closely resembles that of *Rhaphiodon*. The *abductor superficialis* is divided by a tendinous sheet that inserts along the proximal edges of the pectoral rays. The *arrector ventralis* runs from the cleithrum to insert via long tendons on to the first and second pectoral rays. I am unable to find the equivalent of the small 'depressor' muscle described in the Cynodontini (see p. 221).

The long dentary has the symphysial tip drawn out into a tooth-like process (see p. 244). The hyoid bars, urohyal and first basihyal are of similar shape to those elements in *Rhaphiodon*. The gill rakers of *Macrochirichthys* are reduced (as in *Rhaphiodon*); the pharyngeal teeth are in two rows and are thin and sharply pointed (an unusual feature among the cyprinids).

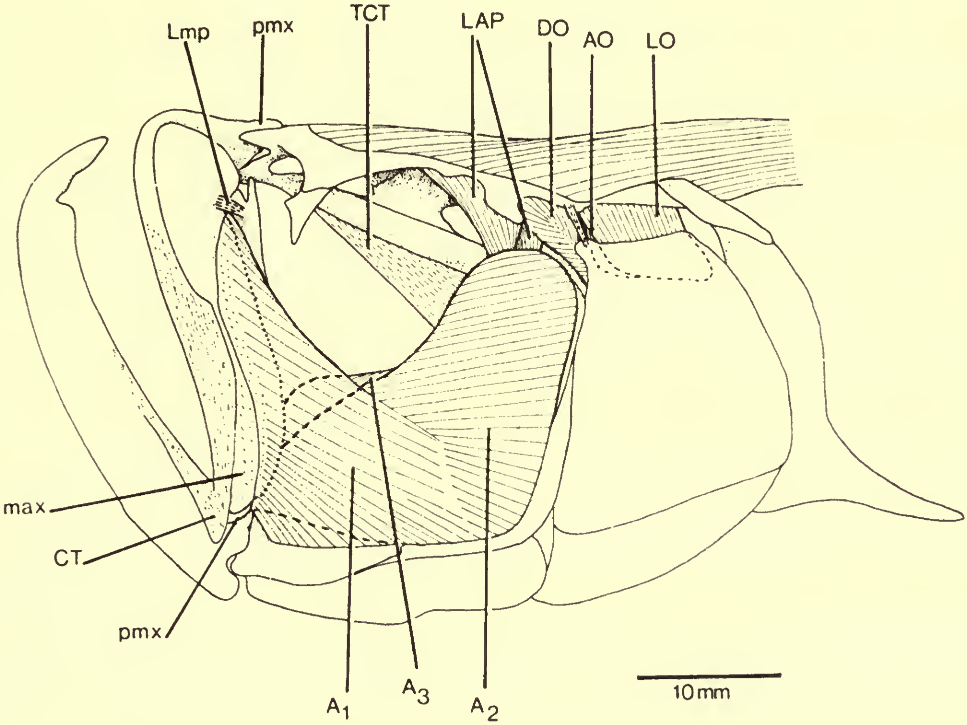


FIG. 23. *Macrochirichthys macrochir*, superficial facial musculature, lateral view. The dotted line indicates the border of the maxilla, the thick dashed lines, the borders of A_2 and A_3, and those on the operculum, the areas of the *levator* and *adductor operculi*.

The parasphenoid is straight and thickened; the orbito-sphenoid is sutured to the parasphenoid (features shown by *Rhaphiodon*).

One difference to be noted is that a ligament connects the pterotic to the operculum and not to the preoperculum, as in *Rhaphiodon*.

Another parallel feature shared with the characoid is the presence of many long intermuscular bones. However, these are not distributed throughout the *epaxialis* but are orientated cranio-caudally along the bases of the neural spines (the more

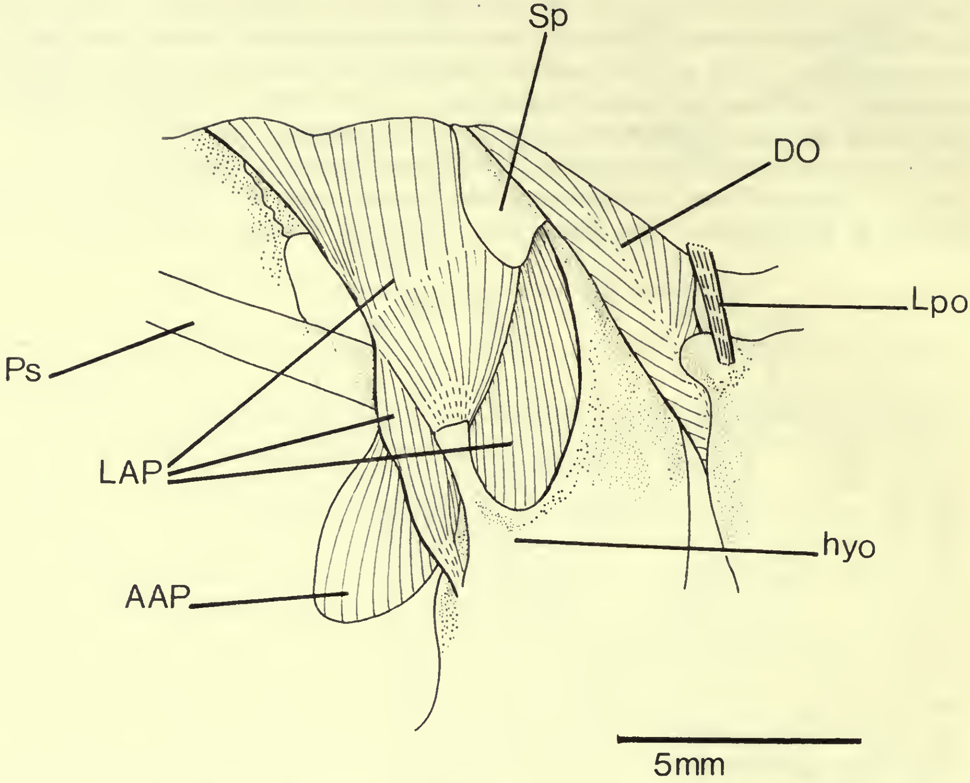


FIG. 24. *Macrochirichthys macrochir*, lateral view of the dorsal aspect of the hyomandibula showing the various insertions of the *levator arcus palatini*.

usual situation). Anteriorly they extend as bundles from the pterotic (as in *Rhaphiodon*).

One peculiar feature of *Macrochirichthys* is the development of the anterior supraneurals (predorsal bones). The first, second and third are thin, elongate structures, the first appearing almost to articulate with the long third neural spine (Fig. 25). This series of bones together forms a firm but flexible arc. This arrangement suggests a counteractant to stresses similar to those believed to occur in *Rhaphiodon* (p. 225) and again is indicative of some backward and upward movement of the skull when the fish is capturing its prey.

The single large symphysial 'tooth' of *Macrochirichthys* possibly performs a more manipulative function than do the slender teeth of *Rhaphiodon* (p. 225). Behind this symphysial projection the dentary is indented, indicating that the prey may be held transversely. A similar strong tooth-like process and jaw indentation can be found in other cyprinoids, e.g. *Opsariichthys uncirostris*, *Barilius bola* and some *Paralaubuca* species.

No stomach contents were present in any of the three specimens of *Macrochirichthys* examined.

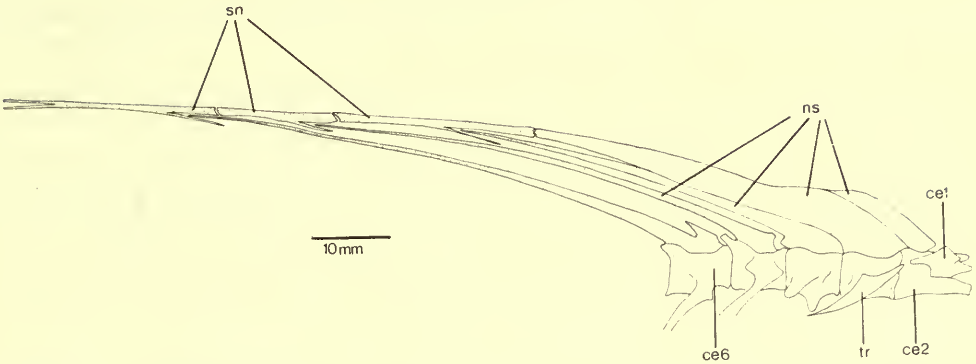


FIG. 25. *Macrochirichthys macrochir*, lateral view (right) of the anterior part of the vertebral column.

The facial musculature of *Macrochirichthys* closely resembles that of *Opsariichthys* (see Takahasi, 1925; Winterbottom, 1974). Furthermore, a quadrate-metapterygoid fenestra is present. This feature was considered by Greenwood *et al.* (1966) to be a primitive character for the cyprinoids. However, Gosline (1973) has pointed out that the fenestra has a functional significance in providing increased area for the *adductor mandibulae*, that it has probably evolved several times over, and that it is the form of the architecture of the suspensorium in which the fenestra has developed that is the indicator of relationship.

The fenestra in *Macrochirichthys* is small compared with that in *Rhaphiodon* and the actual size of the opening appears to have little to do with the degree of development of the *adductor mandibulae* (as observed in other characoids). The presence of the fenestra undoubtedly confers a greater mobility on the suspensorial elements, enabling them to reorientate more readily to the stresses induced by a highly developed (and developing) muscle system.

Macrochirichthys is a highly specialized cyprinid which may have evolved from the same ancestral lineage as did *Opsariichthys*. It is hoped to test this speculation when further material is available.

REFERENCES

ALEXANDER, R. McN. 1964. Adaptation in the skull and cranial muscles of South American characinoid fish. *J. Linn. Soc. (Zool.)*, **45** : 169–190.

—— 1965. Structure and function in the catfish. *J. Zool. Lond.* **148** : 88–152.

—— 1967. *Functional design in fishes*. London.

—— 1968. *Animal mechanics*. London.

—— 1970. Mechanics of the feeding action of various teleost fishes. *J. Zool., Lond.* **159** : 1–15.

ANKER, G. C. 1974. Morphology and kinetics of the head of the stickleback *Gasterosteus aculeatus*. *Trans. zool. Soc. Lond.* **32** : 311–416.

ARAMBURU, A. S. A. DE 1953. Contribución a la sistemática de los peces carácidos llamados 'Dientudos'. *Notas Mus. La Plata*, **16** (Zool.) (145) : 297–320.

BOESEMAN, M. 1952. A preliminary list of Surinam fishes not included in Eigenmann's enumeration of 1912. *Zool. Med. Leiden*, **31** (17) : 179–200.

BÖHLKE, J. E. 1955. Studies on fishes of the family Characidae No. 9. Notes on the distribution, variation and type locality of *Gnathocharax steindachneri* Fowler. *Notul. nat.* **277** : 1–14.

—— 1958. Studies on fishes of the family Characidae—No. 14. A report on several extensive recent collections from Ecuador. *Proc. Acad. nat. Sci. Philad.* **110** : 1–121.

CAMPOS, A. A. 1945. Contribuição ao conhecimento das especies Brasileiras do genêro *Hydrocynus* e afins. *Archos Zoo. Est. S. Paulo*, **4**, art. 12 : 467–484.

DIETZ, P. A. 1914. Beiträge zur Kenntnis der Kiefer- und Kiemenbogenmuskulatur der Teleostier. I. Die Kiemenbogenmuskulatur der Acanthopterygii. *Mitt. zool. Stn Neapel*, **22** (4) : 99–162.

EATON, T. H. 1935. The evolution of the upper jaw mechanism in teleost fish. *J. Morph.* **134** (2) : 131–140.

EDGEWORTH, F. H. 1935. *The cranial muscles of vertebrates.* Cambridge.

EIGENMANN, C. H. 1907. Fowler's 'Heterognathus fishes' with a note on the Stethaprioninae. *Amer. Nat.* **41** : 767–772.

—— 1909. The fresh-water fishes of Patagonia, and an examination of the Archiplata–Archhelenis theory. *Rep. Princeton Univ. Exped. Patagonia* **3** (1) (Zool.) : 225–372.

—— 1910. Catalogue of the fresh-water fishes of tropical and south temperate America. *Rep. Princeton Univ. Exped. Patagonia* **3** (1) (Zool.) : 375–511.

—— 1912a. The fresh-water fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. *Mem. Carneg. Mus.* **5** (67) : 1–578.

—— 1912b. Some results from an ichthyological reconnaissance of Colombia, South America. *Indiana Univ. Stud.* **10** (8) : 1–27.

—— 1916. New and rare fishes from South American rivers. *Ann. Carneg. Mus.* **10** (1–2) : 77–86.

FOWLER, H. W. 1906. Further knowledge of some heterognathus fishes, part I. *Proc. Acad. nat. Sci. Philad.* **58** (2) : 293–351.

—— 1948–1951. Os peixes de agua doce do Brasil. Vol. I. *Archos Zoo. Est. S. Paulo*, **6** : 1–204.

—— 1958. Some new taxonomic names of fishlike vertebrates. *Notul. nat.* **310** : 1–16.

GERY, J. 1959. Contributions à l'étude des poissons Characoïdes (Ostariophysi) (II) *Roeboexodon* gen. n. de Guyana, redescription de *R. guyanensis* (Puyo, 1948), et relations probables avec les formes voisines. *Bull. Mus. natn. Hist. nat. Paris* (2) **31** (4) : 345–352.

—— 1963. Essai sur les affinités phylogénétiques des *Agoniates* et l'origine des Characidae, à propos de la description d'une forme nouvelle de l'Amazone péruvienne : *Agoniates ladigesi* (Contr. No. 22). *Mitt. hamb. zool. Mus. Inst.* **90** : 265–284.

—— 1966. *Hoplocharax goethei* a new genus and species of South American characoid fishes, with a review of the sub-tribe Heterocharacini. *Ichthyologia*, **38** (3) : 281–296.

—— 1972a. Corrected and supplemented descriptions of certain characoid fishes described by Henry W. Fowler, with revisions of several of their genera. *Stud. Neotrop. Fauna*, **7** : 1–35.

—— 1972b. Poissons characoïdes des Guyanaes. I. Généralités. II. Famille des Serrasalmidae. *Zool. Verh., Leiden*, **122** : 1–248.

—— & VU-TAN-TUE. 1963. Définition de *Cynopotamus* Val. et genres voisins (Pisces, Characoidei). *Bull. Mus. natn. Hist. nat. Paris*, (2) **35** (3) : 238–246.

GILL, T. 1871. On some new species of fishes obtained by Prof. Orton, from the Maranon or Upper Amazon and Napo rivers. *Proc. Acad. nat. Sci. Philad.* : 92–93.

GOSLINE, W. A. 1973. Considerations regarding the phylogeny of cypriniform fishes, with special reference to structures associated with feeding. *Copeia*, 1973 (4) : 761–776.

GREENWOOD, P. H. 1971. Hyoid and ventral gill arch musculature in osteoglossomorph fishes. *Bull. Br. Mus. nat. Hist.* (Zool.), **22** (1) : 1–55.

—— ROSEN, D. E., WEITZMAN, S. H., & MYERS, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* **131** : 339–456.

GREENWOOD, P. H. & THOMSON, K. S. 1960. The pectoral anatomy of *Pantodon buchholzi* Peters (a fresh-water flying fish) and the related Osteoglossidae. *Proc. zool. Soc. Lond.* **135** (2) : 283–302.

GREGORY, W. K. & CONRAD, G. M. 1938. The phylogeny of the characin fishes. *Zoologica*, **23** (4) : 319–360.

GRENHOLM, A. 1923. *Studien über die Flossenmuskulatur der Teleostier.* Doctoral dissertation, University of Uppsala, 296 pp.

HOLMQUIST, O. 1911. Studien in der von N.N. Trigeminus und Facialis innervierten Muskulatur der Knockenfische. II. Zur vergleichenden Morphologie der M.M. Intermandibularis, Protractor Hyoidei und Hyohyoideus. *Acta Univ. Lund* N.S. **7** : 47–79.

KAMPF, W. D. 1961. Vergleichende Funktions-morphologisches Untersuchungen an den Viscerocranien einiger räuberisch lebender Knockenfische. *Zool. Beitr.* N.F. **6** (3) : 391–496.

LIEM, K. F. 1967. A morphological study of *Luciocephalus pulcher*, with notes on gular elements in other recent teleosts. *J. Morph.* **121** : 103–133.

LÜLING, K. H. 1972. Der grösste Susswasserfisch. *Fischerei* (12) : 18.

MCALLISTER, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *Bull. natn. Mus. Can.*, Biol. ser., **77** no. 221 : 1–239.

MATTHES, H. 1963. A comparative study of the feeding mechanism of some African Cyprinidae. *Bijdr. Dierk.* **33** : 1–36.

MENEZES, N. A. 1974. Redescription of the genus *Roestes* (Pisces, Characidae). *Papeis Dep. Zool. S. Paulo*, **27** (17) : 219–225.

MILES, C. 1947. *Los peces del Rio Magdalena.* Public. Minist. Econ. Bogota, Colombia.

MILLARD, N. A. H. 1966. Contributions to the functional morphology of fishes. Pt. 1. Introduction. *Zoologica Afr.* **2** : 37–43.

MYERS, G. S. 1927. Descriptions of new South American fresh-water fishes collected by Dr Carl Ternetz. *Bull. Mus. comp. Zool. Harv.* **68** (3) : 107–135.

—— 1949. The family name of the Characid fishes. *Copeia*, **1949** (3) : 195–204.

NELSON, E. M. 1949. The swim bladder and Weberian apparatus of *Rhaphiodon vulpinus* Agassiz, with notes on some additional morphological features. *J. Morph.* **84** (3) : 395–523.

NELSON, G. J. 1967. Branchial muscles in some generalized teleostean fishes. *Acta zool. Stockh.* **48** : 277–288.

NURSALL, J. R. 1956. The lateral musculature and the swimming of fish. *Proc. zool. Soc. Lond.* **126** (1) : 127–143.

OSSE, J. W. M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.) : an electromyographic study. *Neth. J. Zool.* **19** (3) : 289–392.

REGAN, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidea. *Ann. Mag. nat. Hist.* (8) **8** : 13–32.

ROBERTS, T. R. 1967. Tooth formation and replacement in characoid fishes. *Stanford ichthyol. Bull.* **8** (4) : 231–247.

—— 1969. Osteology and relationships of characoid fishes, particularly the genera *Hepsetus, Salminus, Hoplias, Ctenolucius* and *Acestrorhynchus*. *Proc. Calif. Acad. Sci.* (4) **36** (15) : 391–500.

—— 1970. Scale-eating American characoid fishes, with special reference to *Probolodus heterostomus*. *Proc. Calif. Acad. Sci.* (4) **38** (20) : 383–390.

—— 1973a. Osteology and relationships of the Prochilodontidae, a South American family of characoid fishes. *Bull. Mus. comp. Zool. Harv.* **145** (4) : 213–235.

—— 1973b. Interrelationships of ostariophysans. In *Interrelationships of Fishes*, Greenwood, P. H., Miles, R. S., & Patterson, C. (eds) : 373–395. London and New York.

—— 1975. Osteology and classification of the neotropical characoid fishes of the families Hemiodontidae (including Anodontinae) and Paradontidae. *Bull. Mus. comp. Zool. Harv.* **146** (9) : 411–472.

ROSEN, D. E. 1970. A new tetragonopterine characid fish from Guatemala. *Am. Mus. Novit.* no. 2435 : 1–17.

Rosen, D. E. 1972. Origin of the characid fish genus *Bramocharax* and a description of a second, more primitive, species in Guatemala. *Am. Mus. Novit.* no. 2500 : 1–21.

Schultz, L. P. 1950. Review of thirteen genera of South American fishes in the subfamilies Cynodontinae, Hepsetinae, and Characinae with a description of a new Cyrtocharax. *Studies honoring Trevor Kincaid.* Univ. Washington, Seattle : 43–73.

Smith, H. M. 1945. The fresh-water fishes of Siam, or Thailand. *Bull. U.S. natn. Mus.* **188** : 1–622.

Starks, E. C. 1930. The primary shoulder girdle of the bony fishes. *Stanf. Univ. Publs biol. Sci.* **6** (2) : 1–92.

Takahasi, N. 1925. On the homology of the cranial muscles of the cypriniform fishes. *J. Morph.* **40** : 1–109.

Tchernavin, V. V. 1953. *The feeding mechanism of a deep sea fish,* Chauliodus sloanei *Schneider.* London.

Travassos, H. 1946. Discussão sôbre os gêneros 'Cynodon' Spix 1829 e 'Rhaphiodon' Agassiz 1829, com novo nome de subfamilia (Classe Actinopterygii – Ordem Ortareophysii (*sic*)). *Summa brasil. Biol* (Año I) **1** (9) : 129–141.

—— 1951–52. Catalogo dos gêneros e subgêneros da subordem Characoidei (Actinopterygii – Cypriniformes). Reprinted from *Dusenia,* **2** (3–6) and **3** (2–6), 158 pp.

Vetter, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermuskulatur der Fische. *Jena Z. Naturw.* **12** : 431–550.

Walls, E. W. 1960. The microanatomy of muscle. In : *The structure and functions of muscle,* G. H. Bourne (ed.), **1** : 21–59. New York & London.

Weinmann, J. P. & Sicher, H. 1947. *Bone and bones ; fundamentals of bone biology.* London.

Weitzman, S. H. 1962. The osteology of *Brycon meeki,* a generalized characid fish, with an osteological definition of the family. *Stanford ichthyol. Bull.* **8** (1) : 3–77.

—— 1964. Osteology and relationships of South American characid fishes of the subfamilies Lebiasininae and Erythrininae with special reference to subtribe Nannostomina. *Proc. U.S. natn. Mus.* **116** (3499) : 127–170.

Whitehead, P. J. P. & Myers, G. S. 1971. Problems of nomenclature and dating of Spix and Agassiz's *Brazilian fishes* (1829–1831). *J. Soc. Biblphy nat. Hist.* **5** (6) : 478–497.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the teleostei. *Proc. Acad. nat. Sci. Philad.* **125** (12) : 225–317.

Wu, Hsien-Wen. 1964. *Cyprinid fishes of China,* **1**. Shanghai.

G. J. Howes
Department of Zoology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.)
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepède, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay Recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. Pp. 245; 33 Plates, 47 Text-figures. 1973. £10.80.
5. WHITEHEAD, P. J. P. The Clupeoid Fishes of the Guianas. Pp. 227; 72 Text-figures. 1973. £9.70.
6. GREENWOOD, P. H. The Cichlid Fishes of Lake Victoria, East Africa: the Biology and Evolution of a Species Flock. Pp. 134; 1 Plate, 77 Text-figures. 1974. £3.75.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

DESIGNATION OF LECTOTYPES OF SOME OSTRACODS FROM THE CHALLENGER EXPEDITION

BRITISH MUSEUM
GENERAL
01 JUN 1976
LIBRARY
NATURAL HISTORY

H. S. PURI
AND
N. C. HULINGS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 5
LONDON : 1976

DESIGNATION OF LECTOTYPES OF SOME OSTRACODS FROM THE CHALLENGER EXPEDITION

B. M. S. MUSEUM
GENERAL
01 JUN 1976
LIBRARY
NATURAL HISTORY

BY
HARBANS S. PURI
Florida Bureau of Geology
AND
NEIL C. HULINGS
University of Jordan

Pp. 249–315; 27 *Plates*; 14 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 5
LONDON : 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 29, *No.* 5, *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Zool.)

ISSN 0007-1498

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 27 May, 1976 *Price* £8·50

DESIGNATION OF LECTOTYPES OF SOME OSTRACODS FROM THE CHALLENGER EXPEDITION

By H. S. PURI and N. C. HULINGS

CONTENTS

	Page
SYNOPSIS	254
INTRODUCTION	254
GENUS *Phlyctenophora*	
P. zealandica Brady	256
GENUS *Aglaia*	
A. clavata Brady	256
A. (?) *meridionalis* Brady	257
A. (?) *obtusata* Brady	257
A. (?) *pusilla* Brady	257
GENUS *Pontocypris*	
P. simplex Brady	258
P. (?) *subreniformis* Brady	258
GENUS *Argilloecia*	
A. eburnea Brady	259
(?) *A. badia* Brady	259
GENUS *Macrocypris*	
M. canariensis Brady	260
M. setigera Brady	260
M. similis Brady	260
M. tenuicauda Brady	261
M. tumida Brady	261
GENUS *Bythocypris*	
B. elongata Brady	262
B. reniformis Brady	262
GENUS *Bairdia*	
B. abyssicola Brady	263
B. attenuata Brady	263
B. exaltata Brady	264
B. expansa Brady	264
B. fortificata Brady	264
B. globulus Brady	265
B. hirsuta Brady	265
B. minima Brady	266
B. simplex Brady	266
B. villosa Brady	266
B. woodwardiana Brady	267
GENUS *Cythere*	
C. acanthoderma Brady	267
C. acupunctata Brady	268
C. arata Brady	268
C. bicarinata Brady	269

Page
C. circumdentata Brady 269
C. clavigera Brady 270
C. craticula Brady 271
C. cristatella Brady 271
C. cumulus Brady 271
C. curvicostata Brady 272
C. cytheropteroides Brady 272
C. dasyderma Brady 273
C. dictyon Brady 273
C. dorsoserrata Brady 274
C. ericea Brady 275
C. exfoveolata Neviani 275
C. exilis Brady 276
C. falklandi Brady 276
C. flabellicostata Brady 276
C. floscardui Brady 277
C. fulvotincta Brady 277
C. hardingi nom. nov. 277
C. impluta Brady 278
C. inconspicua Brady 278
C. irpex Brady 278
C. irrorata Brady 279
C. kerguelenensis Brady 279
C. (?) *laganella* Brady 280
C. lauta Brady 280
C. lepralioides Brady 280
C. lubbockiana Brady 281
C. mackenziei nom. nov. 281
C. moseleyi Brady 281
C. murrayana Brady 282
C. obtusalata Brady 282
C. packardi Brady 282
C. papuensis Brady 283
C. parallelogramma Brady 284
C. patagoniensis Brady 284
C. quadriaculeata Brady 284
C. radula Brady 285
C. rastromarginata Brady 286
C. sabulosa Brady 286
C. scalaris Brady 287
C. scintillulata Brady 287
C. securifer Brady 288
C. (?) *serratula* Brady 288
C. scabrocuneata Brady 289
C. squalidentata Brady 289
C. stolonifera Brady 289
C. subrufa Brady 290
C. suhmi Brady 290
C. sulcatoperforata Brady 291
C. torresi Brady 292
C. tricristata Brady 292
C. tetrica Brady 293
C. velivola Brady 293

Page
C. vellicata Brady 294
C. viminea Brady 294
C. wyvillethomsoni Brady 295
GENUS *Krithe*
K. hyalina Brady 295
K. producta Brady 295
K. tumida Brady 296
GENUS *Loxoconcha*
L. africana Brady 296
L. anomala Brady 297
L. australis Brady 297
L. honoluliensis Brady 297
L. pumicosa Brady 298
L. subrhomboidea Brady 298
GENUS *Xestoleberis*
X. africana Brady 299
X. expansa Brady 299
X. foveolata Brady 300
X. granulosa Brady 300
X. nana Brady 301
X. setigera Brady 301
X. tumefacta Brady 302
X. variegata Brady 302
GENUS *Cytherura*
C. clavata Brady 303
C. clausi Brady 303
C. costellata Brady 304
C. cribrosa Brady 304
C. cryptifera Brady 304
C. curvistriata Brady 304
C. lilljeborgi Brady 304
C. mucronata Brady 305
GENUS *Cytheropteron*
C. abyssorum Brady 305
C. (?) *angustatum* Brady 305
C. assimile Brady 306
C. fenestratum Brady 306
C. mucronalatum Brady 307
C. patagoniense Brady 307
C. scaphoides Brady 307
C. wellingtoniense Brady 308
GENUS *Bythocythere*
B. arenacea Brady 308
B. (?) *exigua* Brady 309
B. pumilio Brady 309
B. velifera Brady 309
GENUS *Pseudocythere*
P. fuegiensis Brady 309
GENUS *Cytherideis*
C. laevata Brady 310
GENUS *Xiphichilus*
X. (?) *arcuatus* Brady 310
X. complanatus Brady 311

Page
GENUS *Polycope*
P. cingulata Brady 311
P. (?) *favus* Brady 311
GENUS *Cytherella*
C. cribrosa Brady 312
C. dromedaria Brady 312
C. irregularis Brady 312
C. lata Brady 313
C. latimarginata Brady 313
C. venusta Brady 313
REFERENCES 314

SYNOPSIS

Syntype material of recent ostracods described by G. S. Brady from the Challenger Expedition and deposited in the British Museum (Natural History) and the Hancock Museum, Newcastle upon Tyne, is redescribed. Lectotypes are selected where appropriate and topotypic material identified. Neotypes are established for *Xestoleberis tumefacta* Brady, *Bythocythere velifera* Brady and *Cytherella latimarginata* Brady. New names are proposed for *Cythere ovalis* Brady and *C. pyriformis* Brady.

INTRODUCTION

IN order to stabilize ostracod nomenclature, one of us (H. S. P.) initiated a restudy and redescription of the classic European collections of G. W. Müller, G. S. Brady and G. O. Sars. The present contribution is a study of some syntype material deposited in the British Museum (Natural History) and the Hancock Museum, Newcastle upon Tyne. A complete list of species collected during the voyage of the H.M.S. *Challenger* and catalogued at the British Museum (Natural History) was prepared by Dr R. H. Bate (see Bate, 1963).

We would like to express our gratitude to Dr J. P. Harding, formerly Keeper of Zoology, Mrs Patricia Barker and Dr K. G. McKenzie for their encouragement; and to Dr R. H. Bate, Dr K. G. McKenzie, Mr G. Bennell and Miss Ann Gurney for editorial assistance. The stereoscan photographs for Plates 26 and 27 were taken by Miss Gurney. Through the courtesy of Mr A. M. Tynan, Curator, The Hancock Museum, Newcastle upon Tyne, we were able to examine Brady's syntype material deposited in the Hancock Museum. Dr H. V. Howe kindly made available to us his exhaustive index on ostracods. We wish to thank Dr R. H. Benson for critically reading the manuscript and offering helpful comments. The study of Brady's Challenger ostracods was supported by NSF Grant GB 6706.

The descriptive notes which follow the designation of each lectotype are meant to supplement the descriptions given by Brady. The species are arranged in the text and the plates in the same order as they appear in the Challenger monograph and we have used Brady's nomenclature except for two homonyms which are renamed. Short synonomies are given with each species.

Originally it was planned to prepare scanning electron micrographs of the British Museum (Natural History) types, but it was decided not to use this method for fear of damaging the specimens. Consequently, photographs were taken by Dr

R. H. Benson at the Smithsonian Institution in Washington, and these are published as Pls 1–25. Through the kindness of Dr R. H. Bate, we were able to obtain a small portion of the original Challenger sediment samples. Specimens obtained from these samples were used to supplement Brady's syntype material.

Scanning electron photomicrographs of these specimens were prepared by Mr Ron Parker, in Tallahassee, and at the Department of Geology, University of Delaware, Newark, Delaware, through the courtesy of Dr F. W. Swain. These are lodged at the British Museum (Natural History) together with the topotypic material. Two plates of scanning photomicrographs are included in this paper. Lectotypes of seven species described by Brady (1880) have already been established. Type specimens of *Cythere scabrocuneata* Brady were established by Harding & Sylvester-Bradley (1953). Benson (1971) established an early instar as lectotype for *Cythere squalidentata* Brady (considered by Benson as a *nomen dubium*), and he subsequently (Benson, 1972) established lectotypes for *Cythere arata* Brady, *Cythere dictyon* Brady, *Cythere rastromarginata* Brady, *Cythere radula* Brady and *Cythere vimea* Brady. Illustrations of the above lectotypes established by Benson appear in this paper.

Richard H. Benson prepared the following text on photographic techniques.

'The photographic equipment used was the Leitz Aristophot Microscope with Ultrapac lenses and 35 mm camera. The specimens were placed either dry (for incident illumination) or in immersion (for transmitted and black light) on glass so that extraneous light would pass through rather than be reflected by the background. A single light source was used for incident illumination in conjunction with a paper diffusing ring held close to the specimen. The background of incident light photographs could be varied from light to dark with the aid of an off-centre substage light and variable rheostat. Conventional techniques were used for the transmitted light photographs, but the lenses had a longer working distance and greater depth of field than those usually employed in photomicrography. Inadequate depth of field still is a limitation to the use of conventional photomicrography for illustration of ostracods. One will notice this in many of the figures in the present work. Every photograph was a compromise of some kind, especially with the large or thick specimens.

'With the use of transmitted light and immersion of the specimen in water or glycerine many features that Brady did not illustrate could be seen. Many muscle-scar patterns, hinges, surface ornament, and marginal area features are now shown for comparison with specimens collected elsewhere. It is regretted that all of these characters could not be illustrated by photography for all forms. Attempts were made to obtain photographs of these features wherever they could be seen.'

Illustration was confined to new species found and described by Brady from the Challenger samples. There are many others which had been previously described and which he identified. Four of these are illustrated on Pl. 25. These were thought to have special interest and were included while the opportunity was at hand. These include *Cythere melobesioides* Brady, 1869, *Cythere cymba* Brady, 1869, *Cythere polytrema* Brady, 1878, and *Cythere euplectella* Brady, 1869.

The following species have not been illustrated as specimens could not be found either in the collection or in the topotype material: *Cythere fortificata, Bythocypris* *compressa* and *Cytherura obliqua*. Type specimens of *Cytherella latimarginata* were lost and a neotype is selected.

There are some discrepancies between Brady's description of stations and the narrative of the Challenger cruise (Tizard *et al.*, 1885). Under each type locality, data provided by Brady on the slides are given and the additional data which are documented in the narrative are given in parentheses after each station.

Genus ***PHLYCTENOPHORA***

Phlyctenophora zealandica Brady

(Pl. 1, figs 17, 18)

Phlyctenophora zealandica Brady, 1880 : 33, pl. 3, figs 1a–m.

Figured specimen. Articulated carapace (split), BM 81.5.7. Length 0·88 mm ; height 0·38 mm. *Type locality:* Humboldt Bay, Papua, 37 fathoms.

Description. *Shape and ornamentation* essentially as given by Brady (1880). *Inner lamella:* anterior and posterior vestibula present, latter larger ; ventral shelf present. *Marginal pore canals* anteriorly branching, several main canals each giving off numerous smaller canals ; posteriorly, simple straight canals. *Hinge* difficult to discern. Right valve apparently with anterior and posterior sockets and median bar.

Remarks. Pl. 1, figs 17, 18 represent the specimen labelled by Brady as '*Phlyctenophora zealandica*' in the British Museum collection and may not represent Brady's concept of this species. Brady also figured the soft parts of this species. The selection of a lectotype is deferred until living specimens are found in adequate quantity and described. *Topotypic material:* disarticulated left and right valves, BM 1974.246.

Genus ***AGLAIA***

Aglaia clavata Brady

(Pl. 2, figs 16, 17)

Aglaia clavata Brady, 1880 : 34, pl. 6, figs 4a–d.

Lectotype. Disarticulated left and right valves, BM 81.5.1 (separated after photography). Length of articulated carapace 0·56 mm ; greatest height 0·23 mm. *Type locality:* Wellington Harbour, New Zealand (trawl-net).

Description. *Shape and ornamentation* as given by Brady (1880), see Pl. 2, figs 16 and 17. *Inner lamella:* marginal zone narrow in anterior and posterior ends ; wide along middle two-thirds of ventral margin. Anterior and posterior vestibula large. Line of concrescence irregular. *Marginal pore canals:* anterior canals numerous and simple. No pore canals seen on ventral or posterior end. *Hinge* adont. *Central muscle scars:* five scars divided into an anterior row of three and two posterior.

***Aglaia* (?) *meridionalis* Brady**

(Pl. 20, figs 4–6)

Aglaia (?) *meridionalis* Brady, 1880 : 34, 35, pl. 30, figs 7a–d.

LECTOTYPE. Left valve with outer margin fractured, BM 1961.12.4.63. Length 0·65 mm ; height 0·28 mm. *Type locality:* Stat. 316, Stanley Harbour, Falklands, 6 fathoms. (51°32′0″N, 58°06′0″W, dredged, 4 fathoms, mud, surface temp. 51·2°F, February 3, 1876.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). *Inner lamella* not distinguishable on lectotype. *Central muscle scars:* see Pl. 20, fig. 6.

***Aglaia* (?) *obtusata* Brady**

(Pl. 20, figs 7, 8)

Aglaia (?) *obtusata* Brady, 1880 : 35, pl. 30, figs 8a–d.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.4 (separated after photography). Right valve : length 0·55 mm ; height 0·27 mm ; left valve : length 0·52 mm ; height 0·24 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island. (49°08′0″S, 70°12′0″E, dredged, 20–50 fathoms, dark mud, January 9, 1874.)

DESCRIPTION. *Shape* as given by Brady (1880) for right valve. Left valve smaller, anterior and posterior ends less broadly rounded than right valve, ventral surface sinuate near middle. *Ornamentation* as given by Brady (1880). *Inner lamella:* line of concrescence irregular ; anterior and posterior vestibula, the former large and the latter reduced, marginal area narrow anteriorly and posteriorly, wide ventrally. *Marginal pore canals* numerous and simple at anterior end, few and simple, some false at posterior end. *Hinge* adont. *Central muscle scars:* anterior row of three and posterior row of two making a total of five scars. *Overlap:* right valve overlaps the left valve.

***Aglaia* (?) *pusilla* Brady**

(Pl. 20, figs 1–3)

Aglaia (?) *pusilla* Brady, 1880 : 34, pl. 30, figs 6a–d.

LECTOTYPE. Disarticulated right and left valves, BM 81.5.2. Right valve : length 0·51 mm ; height 0·22 mm ; left valve : length 0·50 mm ; height 0·20 mm. *Type locality:* Stat. 162, dredged off East Moncœur Island, Bass Strait, 38–40 fathoms. (39°10′30″S, 146°37′0″W, surface temp. 63·2°F, April 2, 1874.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). *Inner lamella:* line of concrescence irregular, anterior and posterior vestibula with anterior larger, marginal area narrow anteriorly and posteriorly, wide ventrally. See Pl. 20, figs 1 and 3. *Marginal pore canals* numerous and simple anteriorly. *Hinge* adont.

Central muscle scars: five scars, vertical row of three anteriorly and two posteriorly. See Pl. 20, fig. 2. *Overlap:* right valve overlaps the left.

REMARKS. Brady (1880, p. 34) found this species only at Stat. 162; sediment sample M-195, which represents this station, yielded a single articulated carapace. *Topotypic material:* a complete carapace, BM 1974.250.

Genus ***PONTOCYPRIS***

Pontocypris simplex Brady

(Pl. 1, figs 6–8)

Pontocypris simplex Brady, 1880: 37, pl. 1, figs 5a–d.

LECTOTYPE. Disarticulated right and left valves of a complete specimen, BM 81.5.4 (separated during photography). Right valve: length 0·62 mm; height 0·31 mm; left valve: length 0·62 mm; height 0·31 mm. *Type locality:* Stat. 344. Off Ascension Island, 71 fathoms.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). *Inner lamella:* large anterior and posterior vestibula. Duplicature widest ventrally. Inner margin coincides with the line of concrescence only ventrally. Ventral margin expanded to form a small shelf in both valves. *Marginal pore canals* short, simple, straight, most numerous anteriorly. A few false canals ventrally. *Hinge* adont. Groove in right valve. *Normal pores* numerous, small, open. *Central muscle scars:* adductor consists of five scars.

Pontocypris* (?) *subreniformis Brady

(Pl. 3, fig. 16)

Pontocypris (?) *subreniformis* Brady, 1880: 38, 39; pl. 7, figs 5a–d, not *Pontocypris* (?) *subtriangularis* Brady, 1880: pl. 15, figs 6a–d (*nom. nud.*).

LECTOTYPE. Disarticulated right and left valves, right valve cracked ventrally, BM 81.5.5 (separated after photography). Right valve: length 0·65 mm; height 0·34 mm; left valve: length 0·62 mm; height 0·34 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape* of left valve as given by Brady (1880), except that on the type, the anterior end is rounded rather than depressed, the posterior is more acutely rounded. Right valve the same but with the dorsal surface more evenly arched. See Pl. 3, fig. 16. *Ornamentation* as given by Brady (1880). *Inner lamella:* anterior and posterior vestibula present with the former the largest, line of concrescence and inner margin coincide ventrally where the lamella is the widest. Ventral margin expanded to form a shelf. *Marginal pore canals* short, straight and simple. *Hinge* adont. Right valve with a groove for the dorsal border of the left valve. *Normal pores* small and open.

Remarks. Brady (1880, pp. 38, 39) described this species from two stations (Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, and Port Jackson). Port Jackson is the type locality of the lectotype. The lectotype resembles Brady's illustration on pl. 7 (figs 5a–d), the topotypes are much longer and may represent forms figured by Brady on pl. 7 (figs 5a–d) as '*subtriangularis*'. Both of these forms belong to *Propontocypris* as shown by muscle scars and other internal features. *Topotypic material:* BM 1974.249.

Genus ***ARGILLOECIA***

Argilloecia eburnea Brady

(Pl. 2, figs 5, 6)

Argilloecia eburnea Brady, 1880 : 40, pl. 4, figs 1–15.

Lectotype. Left valve, BM 80.38.9. Length 0·81 mm; height 0·34 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island, 20–50 fathoms, January 1874.

Description. *Shape and ornamentation* as given by Brady (1880). *Inner lamella:* anterior and posterior vestibula large, marginal area narrow. *Marginal pore canals* simple. *Hinge* adont. *Central muscle scars:* five scars, anterior vertical row of three and posterior row of two. See Pl. 2, fig. 6.

Remarks. Brady (1880, p. 40) reported this species as occurring 'plentifully' from two dredgings from Kerguelen Island–Balfour Bay (20–50 fathoms) and off Christmas Harbour (120 fathoms). The lectotype is from Stat. 149 (Balfour Bay) and the topotypic specimen was obtained from sediment sample M-183 which represents the Christmas Harbour dredging. *Topotypic material:* a complete carapace, BM 1974.251.

Argilloecia badia Brady

(Pl. 27, figs 1, 2)

Argilloecia badia Brady, 1880 : 40, pl. 6, figs 3a–d.

Figured specimen. Complete carapace, BM 1974.252. Length 0·84 mm; height 0·40 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

Remarks. Brady (1880) reported this species from Port Jackson. Sediment sample M-198 yielded several specimens and a right valve is figured on Pl. 27. The type specimens of this species were evidently lost. There are no specimens in British Museum (Natural History) and none are at the Hancock Museum (*fide* letter by Mrs O. Marshall, secretary to Mr A. M. Tynan, Curator, Hancock Museum, dated July 24, 1967, to H. S. Puri). The form questionably identified and figured here is twice as large as the one figured by Brady, 1880 (length 0·4 mm). More material is needed in order to select a neotype.

Genus *MACROCYPRIS*

Macrocypris canariensis Brady

(Pl. 1, figs 15, 16)

Macrocypris canariensis Brady, 1880 : 42, pl. 2, figs 3a–d.

LECTOTYPE. Disarticulated right and left valves. Both valves eroded, BM 81.5.6 (separated after photography). Right valve : length 1·94 mm ; height 0·68 mm ; left valve : length 1·98 mm ; height 0·60 mm. *Type locality:* off Canary Island, 620 fathoms. (28°03′15″N, 17°27′0″W, dredged, surface temp. 64·5°F.)

DESCRIPTION. *Shape and ornamentation* essentially as given by Brady (1880). *Inner lamella:* wide anteriorly and posteriorly with vestibulum present at both ends. Ventral shelf present. *Marginal pore canals* straight, simple. *Hinge* merodont-entomodont. Right valve with anterior and posterior terminal sockets and median bar. Left valve with anterior and posterior terminal teeth and median groove. Teeth, sockets and terminal portions of median bar smooth. *Normal pores* small, open, mostly on ventral half of valves.

Macrocypris setigera Brady

(Pl. 1, figs 1–5)

Macrocypris setigera Brady, 1880 : 43, pl. 1, figs 1a–d.

LECTOTYPE. Left and right valves of a disarticulated specimen, BM 80.38.2 (separated after photography). Right valve : length 1·20 mm ; height 0·50 mm ; left valve : length 1·21 mm ; height 0·54 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880) except for absence of setae. *Inner lamella:* wide anteriorly and posteriorly, narrow ventrally. Line of concrescence and inner margin coincide for a very short distance ventrally. Wide vestibula ventrally. *Marginal pore canals* numerous and branching, some false. Longest ventrally, short anteriorly and posteriorly. See Pl. 1, figs 4 and 5. *Hinge* adont. Left valve with a shallow groove. *Normal pores* numerous, scattered, small open. *Central muscle scars:* see Pl. 1, fig. 3, the complex consists of seven adductor scars.

REMARKS. *Topotypic material:* a complete carapace, BM 1974.245.

Macrocypris similis Brady

(Pl. 1, figs 13, 14)

Macrocypris similis Brady, 1880 : 42, pl. 2, figs 2a–d.

LECTOTYPE. Right valve, BM 80.38.14. Length 1·72 mm ; height 0·62 mm. *Type locality:* Stat. 120, off Pernambuco, 675 fathoms. (8°37′0″S, 34°28′0″W, trawled, red mud, surface temp. 78°F, September 9, 1873.)

DESCRIPTION. *Shape:* Brady's (1880) description appears to be based on a left valve. Present type has an almost straight ventral margin, dorsal gently arched and anterior end evenly rounded. *Ornamentation* as given by Brady (1880). *Inner lamella:* line of concrescence very narrow and coincides with inner margin only ventrally; anterior and posterior vestibula present, ventral shelf narrow. See Pl. 1, fig. 13. *Marginal pore canals* numerous, short, straight, simple. *Hinge* merodont-entomodont. Right valve with anterior and posterior crenulated sockets and smooth median bar. *Normal pores* few, small, open. *Central muscle scars:* see Pl. 1, fig. 14. Dorsal cluster of three and ventral cluster of seven.

REMARKS. *Topotypic material:* a left valve, BM 1974.243, and a complete carapace, BM 1974.244, were recovered from sediment sample M-140 (Stat. 120).

Macrocypris tenuicauda Brady

(Pl. 1, figs 11, 12)

Macrocypris tenuicauda Brady, 1880: 41, 42, pl. 2, figs 1a–f; pl. 3, figs 2a–b.

LECTOTYPE. Left valve, eroded and encrusted, BM 80.38.16. Length 1·70 mm; height 0·60 mm. *Type locality:* Stat. 24, off Culebra Island, West Indies, 390 fathoms. (18°38′30″N, 65°05′30″W, pteropod ooze, surface temp. 76°F, March 25, 1873.)

DESCRIPTION. *Shape:* the present type differs from Brady's (1880) description in the following ways; the anterior end of type is broader and more truncated; the mid-portion of the dorsal surface is gently arched, sinuated anteriorly and gently sloping posteriorly; ventral surface sinuated near anterior. *Ornamentation* as described by Brady (1880). *Inner lamella:* anterior and posterior vestibula present. *Marginal pore canals:* anteriorly, five major canals each giving off numerous branches. Remainder of canals single and straight. *Hinge* merodont-entomodont.

REMARKS. *Topotypic material:* several specimens (BM 1974.242) of this species were recovered from sediment sample M-44 (Stat. 24).

Macrocypris tumida Brady

(Pl. 2, figs 13–15)

Macrocypris tumida Brady, 1880: 43, pl. 6, figs 2a–d.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.17. Right valve: length 0·71 mm; height 0·31 mm; left valve: length 0·71 mm; height 0·28 mm. *Type locality:* Stat. 149, Royal Sound, Kerguelen Island, 28 fathoms. (49°08′0″S, 70°12′0″E, 20 fathoms, dredged, volcanic mud, January 9, 1874.)

DESCRIPTION. *Shape* as described by Brady (1880) except that height is less than one-half length and ventral region is sinuate. *Ornamentation* as described by Brady (1880). *Inner lamella:* line of concrescence irregular throughout, ventrally coincides with the inner margin, large anterior and posterior vestibula present. *Marginal* *pore canals* numerous, straight and simple anteriorly, less numerous ventrally and posteriorly. *Hinge* adont. *Central muscle scars:* adductor scars consist of an anterior vertical row of three and a posterior row of two scars.

Genus ***BYTHOCYPRIS***

Bythocypris elongata Brady

(Pl. 2, figs 11, 12)

Bythocypris elongata Brady, 1880 : 47, pl. 6, figs 1a–c.

Lectotype. Right valve, BM 81.5.8. Length 1·36 mm; height 0·59 mm. *Type locality:* Stat. 335, north of Tristan d'Acunha, 1425 fathoms.

Description. *Shape and ornamentation* as given by Brady (1880). *Inner lamella:* line of concrescence regular, following outer margin. Marginal area narrow. *Hinge* adont. *Normal pores* open and scattered. *Central muscle scars:* four scars, three elongate and aligned in a vertical row anteriorly. Posterior scar rounded.

Bythocypris reniformis Brady

(Pl. 2, figs 7–10; Fig. 1)

Bythocypris reniformis Brady, 1880 : 46, pl. 5, figs 1a–l.

Lectotype. Right valve, BM 80.38.19. Length 1·09 mm; height 0·52 mm. *Type locality:* Stat. 24, north of St Thomas, West Indies, 390 fathoms. (18°38′30″N, 65°05′30″W, dredged, pteropod ooze, surface temp. 76°F, March 25, 1873.)

Description. *Shape and ornamentation* as given by Brady (1880). *Hinge* adont. *Normal pores* open and scattered. *Central muscle scars:* adductor scars arranged in

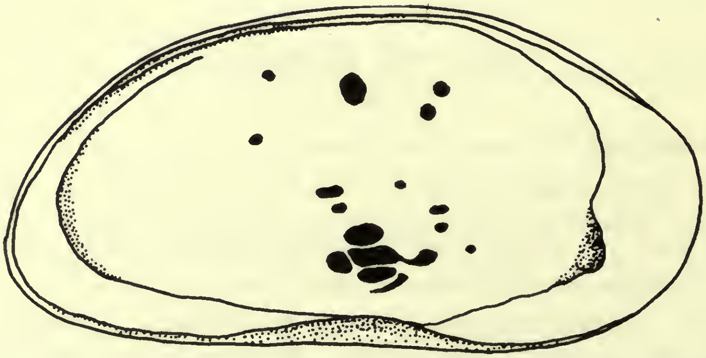


Fig. 1. *Bythocypris reniformis* Brady: interior view of left valve of topotype, BM 1974.255 (× 85).

a vertical row of three horizontal (always split) and a posteroventral scar. Antennal, frontal, mandibular and dorsal are also present (see Fig. 1).

REMARKS. Brady (1880, p. 46) reported this species from Stat. 24 (off Cubebra Island, West Indies, mud), Stats. 120 and 122 (off Prince Edward's Island and off Moncœur Island, Bass Strait). Topotypes were separated from sediment sample M-169 (Prince Edward's Island, 50–150 fathoms) where this species is common. It is also common in Stat. 122 (M-142). *Topotypic material:* a complete carapace, BM 1974.254, and a left valve, BM 1974.255.

Genus ***BAIRDIA***

Bairdia abyssicola Brady

(Pl. 3, fig. 15)

Bairdia abyssicola Brady, 1880 : 52, 53, pl. 7, figs 4a–c.

LECTOTYPE. Right valve, Hancock Museum. Length 1·60 mm; height 0·93 mm. *Type locality:* Stat. 246, North Pacific, 2050 fathoms. (36°10′0″N, 178°0′0″E, trawled, grey ooze, bottom temp. 35·1°F, surface temp. 73·0°F, July 2, 1875.)

DESCRIPTION. *Shape* as given by Brady (1880). *Ornamentation* smooth. *Inner lamella:* anterior vestibule larger than posterior one. *Hinge* with weak terminal teeth. *Central muscle scars:* three elongate scars arranged vertically. Dorsal scar the shortest, the ventral scar the largest, and with a constriction two-thirds toward the posterior. The dorsal scar also has a constriction near the middle.

Bairdia attenuata Brady

(Pl. 5, figs 4–6)

Bairdia attenuata Brady, 1880 : 59, pl. 11, figs 3a–e.

LECTOTYPE. Eroded right valve, BM 80.38.27. Length 1·30 mm; height 0·80 mm. *Type locality:* Stat. 185, Torres Straits, 155 fathoms. (11°35′25″S, 144°02′0″E, dredged, 135 fathoms, coral sand, surface temp. 77°F, August 31, 1874.)

DESCRIPTION. *Shape* as given by Brady (1880), except that the posterior extremity is blunt rather than pointed and the dorsal surface is flat rather than arched. *Ornamentation* obscure because of worn surface. *Inner lamella* widest anteriorly. Anterior and posterior vestibula present. *Hinge:* posterior terminal tooth in right valve. *Central muscle scars:* adductor made up of a subcentral group of eight scars. The anteriormost 'scar' of the ventral row, see Pl. 5, fig. 6, is not a scar but a hole in the shell.

REMARKS. Brady (1880, p. 59) reported this form from the Torres Straits (Stat. 185) and reefs at Honolulu. Topotype specimens have been recovered from sediment sample M-237 (Stat. 185). *Topotypic material:* a right valve, BM 1974.256, and a left valve, BM 1974.257.

Bairdia exaltata Brady

(Pl. 4, figs 12–15)

Bairdia exaltata Brady, 1880 : 51, pl. 9, figs 2a–d.

Lectotype. Right and left valves, BM 81.5.10. Right valve : length 1·24 mm ; height 0·74 mm ; left valve : length 1·28 mm ; height 0·90 mm. *Type locality:* Stat. 218, Bismarck Sea northeast of New Guinea, 1070 fathoms. (2°23′0″S, 144°04′0″E, trawled, blue mud, bottom temp. 36·4°F, surface temp. 84°F, March 1, 1875.)

Description. *Shape and ornamentation* as given by Brady (1880). See Pl. 4, figs 12, 13 for details of right valve. *Inner lamella:* marginal area wide ; vestibule varies in width ; widest anteroventrally, narrowing mid-ventrally, increasing in width in posterior half of ventral region, narrowing again and finally disappearing about mid-posterior. See Pl. 4, figs 12, 13 and 15. *Marginal pore canals* simple, straight and continuous, number about the same from anterior to posterior. *Hinge:* right valve with weak terminal teeth. *Central muscle scars*, see Pl. 4, fig. 14. Also note accessory scars.

Bairdia expansa Brady

(Pl. 5, figs 1–3)

Bairdia expansa Brady, 1880 : 58, 59, pl. 11, figs 2a–e.

Lectotype. Disarticulated right and left valves of a complete carapace, BM 81.5.11. Right valve : length 0·71 mm ; height 0·40 mm ; left valve : length 0·71 mm ; height 0·43 mm. *Type locality:* reef off Honolulu, 40 fathoms, July 1875.

Description. *Shape* as described by Brady (1880) for left valve. See Pl. 5, fig. 3 for right valve. *Ornamentation* as given by Brady (1880) *Inner lamella:* narrow marginal area, vestibule widest at anterior, narrows greatly at ventral sinus (right valve) increases in width again posterior to ventral sinus, then disappears about mid-posterior. See Pl. 5, figs 1 and 3. *Hinge* adont. *Normal pores* open, evenly distributed. *Central muscle scars* about twelve, very irregularly shaped scars. See Pl. 5, fig. 2.

Bairdia fortificata Brady

(Pl. 5, figs 7–9)

Bairdia fortificata Brady, 1880 : 59, pl. 11, figs 4a–b.

Lectotype. Left valve, BM 81.5.12. Length 1·09 mm ; height 0·56 mm. *Type locality:* Stat. 187, off Booby Island, north of Australia. (10°36′0″S, 141°55′0″E, dredged, 6 fathoms, coral mud, surface temp. 77·7°F, September 9, 1874.)

Description. *Shape* as given by Brady (1880). See Pl. 5, fig. 7. *Ornamentation:* see Pl. 5, figs 7 and 8. *Inner lamella:* marginal zone wide, vestibule very reduced and restricted to anterior and posterior extremities. *Marginal pore canals* simple, straight and numerous. *Hinge* adont. Left valve with straight, smooth groove. *Central muscle scars:* see Pl. 5, fig. 8.

REMARKS. The only specimen of this species (a left valve) found by Brady (1880, p. 59) is designated lectotype. Two left valves and a complete carapace were recovered from sediment sample M-242 (Stat. 187). *Topotypic material:* two left valves, BM 1974.271–272.

Bairdia globulus Brady
(Pl. 4, figs 6–11)

Bairdia globulus Brady, 1880 : 54, pl. 9, figs 1a–d.

LECTOTYPE. Right and left valves of an articulated specimen, BM 80.38.34 (separated after photography). Right valve : length 1·05 mm ; height 0·62 mm ; left valve : length 1·09 mm ; height 0·71 mm. *Type locality:* Nares Harbour, Admiralty Islands, 16 fathoms, March 2, 1875.

DESCRIPTION. *Shape* as described by Brady (1880) for left valve. Notable differences between the description by Brady and the left valve of the lectotype include the anterior extremity, the latter not being 'very broadly rounded', absence of teeth at the anterior end and their presence on the posteroventral end, the ventral margin not being considerably arched and the height of the left valve being closer to two-thirds of the length, rather than three-fourths. See Pl. 4, fig. 6 for other features of left valve and Pl. 4, figs 8 and 9 for shape of right valve. *Ornamentation:* 'distinct small impressed puncta' of Brady not present on lectotype. *Inner lamella:* see Pl. 4, figs 6 and 8. *Marginal pore canals* simple and straight. *Hinge:* right valve with weak terminal teeth. *Normal pores* open, evenly distributed. *Central muscle scars:* see Pl. 4, fig. 10.

Bairdia hirsuta Brady
(Pl. 4, figs 4, 5)

Bairdia hirsuta Brady, 1880 : 50, 51, pl. 8, figs 3a–d.

LECTOTYPE. Right valve, BM 80.38.35. Length 1·46 mm ; height 0·90 mm. *Type locality:* Stat. 300, near Juan Fernandez Island, west of Chile, 1375 fathoms. (33°42′0″S, 78°10′0″W, trawled, *Globigerina* ooze, bottom temp. 35·5°F, surface temp. 62·5°F, December 17, 1875.)

DESCRIPTION. *Shape* as given by Brady (1880). *Ornamentation:* smooth and glossy, hairy. *Inner lamella:* marginal zone well developed, anterior and posterior vestibula equal in size. *Hinge* adont. *Central muscle scars:* anteriorly, three elongated scars arranged vertically, plus a single posterior scar.

Bairdia minima Brady

(Pl. 3, figs 17, 18; Pl. 4, figs 1–3)

Bairdia minima Brady, 1880: 53, pl. 7, figs 6a–g.

LECTOTYPE. Right and left valves of a complete carapace, BM 80.38.37. Right valve: length 0·65 mm; height 0·39 mm; left valve: length 0·63 mm; height 0·40 mm. *Type locality:* Port Jackson, Australia, 6 fathoms, April 20, 1874.

DESCRIPTION. *Shape* as described by Brady (1880) for left valve. See Pl. 3, fig. 18, for details of right valve. *Ornamentation* as given by Brady (1880). *Inner lamella*: marginal area very narrow. *Hinge:* right valve 'toothless'. *Normal pores* open and numerous, especially numerous outside the central muscle scar field. *Central muscle scars:* see Pl. 4, fig. 2. The right valve has eight scars, the left valve nine, each valve having two frontal and two mandibular scars.

Bairdia simplex Brady

(Pl. 3, figs 11–14)

Bairdia simplex Brady, 1880: 51, pl. 7, figs 1a–d.

LECTOTYPE. Right and left valves of a complete carapace, BM 81.5.13. Right valve: length 0·49 mm; height 0·78 mm; left valve: length 1·49 mm; height 0·81 mm. *Type locality*: Stat. 151, off Heard Island, 75 fathoms. (52°59′30″S, 73°33′30″E, dredged, volcanic mud, surface temp. 36·2°F, February 7, 1874.)

DESCRIPTION. *Shape* as described by Brady (1880) for left valve. See Pl. 3, figs 11 and 12 for left valve and figs 13 and 14 for right valve. *Inner lamella:* marginal zone wide, vestibule well developed and widest at anterior end, see Pl. 3, figs 12 and 14. *Marginal pore canals* numerous, simple and straight. *Hinge:* right valve 'toothless'. *Normal pores* numerous, open and evenly distributed. *Central muscle scars:* eight somewhat rounded scars in each valve arranged in a circular manner. Mandibular scar appears to be single although it is elongate and constricted near the centre; frontal and other scars distinguishable.

Bairdia villosa Brady

(Pl. 2, figs 1–4)

Bairdia villosa Brady, 1880: 50, pl. 3, figs 3a–b, pl. 5, figs 2a–g, pl. 8, figs 4a–f.

LECTOTYPE. Right and left valves of a complete carapace, BM 80.38.44. Right valve: length 1·30 mm; height 0·80 mm; left valve: length 1·33 mm; height 0·92 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island. (49°08′0″S, 70°12′0″E, dredged, 20 fathoms, volcanic mud, January 9, 1874.)

DESCRIPTION. *Shape* essentially as described by Brady (1880). See Pl. 2, figs 1 and 3. *Inner lamella:* marginal areas widest anteroventrally. Anterior and posterior vestibula well developed. *Marginal pore canals* numerous, straight and simple. *Hinge:* right valve 'toothless'. *Normal pores* open. *Central muscle scars:* see Pl. 2, fig. 2.

REMARKS. Brady (1880, p. 50) reported this species from Stats. 135 and 149; off Christmas Harbour, Kerguelen Island; off Prince Edward's Island and off Moncœur Island, Bass Strait (Stat. 162). This form is common in sediment sample M-169 and a left valve and right valve (with appendages) have been obtained. *Topotypic material:* a right valve, BM 1974.269, and a left valve, BM 1974.270.

Bairdia woodwardiana Brady

(Pl. 4, figs 16–18)

Bairdia woodwardiana Brady, 1880: 57, 58, pl. 11, figs 1a–e.

LECTOTYPE. Right and left valves of a complete specimen, BM 80.38.46. Right valve: length 0·98 mm; height 0·47 mm; left valve: length 0·96 mm; height 0·50 mm. *Type locality:* Stat. 172, off Tongatabu, 18 fathoms. (20°58′0″S, 175°09′0″W, dredged, coral mud, surface temp. 75°F, July 22, 1874.)

DESCRIPTION. *Shape* essentially as described by Brady (1880). See Pl. 4, figs 16 and 18. Note opaque areas. *Ornamentation:* surface very finely punctate. *Inner lamella:* see Pl. 4, figs 16 and 18. Marginal zone widest anteriorly. Anterior vestibule large, posterior very reduced and subparallel to outer margin. *Marginal pore canals* simple, straight. *Normal pores* open, numerous, evenly distributed. *Central muscle scars:* see Pl. 4, fig. 17.

REMARKS. Brady found 'about a dozen' (1880, pp. 57, 58) specimens of this species at a single station. Sediment sample M-220 from this Stat. 172 yielded twelve complete carapaces and detached valves. *Topotypic material:* a complete carapace, BM 1974.258, a left valve, BM 1974.259, and a right valve, BM 1974.260. Additional specimens registered BM 1974.261–8.

Genus ***CYTHERE***

Cythere acanthoderma Brady

(Pl. 11, figs 16–18)

Cythere scabra Brady, 1866 (non Münster), 1866: 380, pl. 61, figs 8a–d.
Cythere acanthoderma Brady, 1880: 104, 105, pl. 18, figs 5a–e.

LECTOTYPE. Left valve of a late instar, BM 80.38.48A. Length 0·99 mm; height 0·59 mm. *Type locality:* Stat. 146, deep sea, east of Prince Edward's Island, 1375 fathoms. (46°46′0″S, 45°31′0″E, trawled, *Globigerina* ooze, bottom temp. 35·6°F, surface temp. 43°F, December 29, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Inner lamella* very narrow. *Marginal pore canals* mostly straight, a few divided marginal pore canals with several false canals. See Pl. 11, fig. 17. *Hinge* holamphidont:

the hinge in the left valve is not completely developed as the type is a late instar. See Pl. 11, fig. 17. *Normal pores* present. *Central muscle scars:* four adductor muscle scars vertically arranged, somewhat elongated. The frontal scar is on the anterior edge of the subcentral tubercle and appears as a small transversely elongated scar.

REMARKS. *Topotypic material:* a complete carapace, BM 1974.277, and a right valve, BM 1974.276, were found in sediment sample M-170 (Stat. 146).

Cythere acupunctata Brady

(Pl. 8, fig. 5)

Cythere acupunctata Brady, 1880 : 68, pl. 14, figs 1a–h.

LECTOTYPE. Whole carapace, BM 80.38.50. Right valve: length 0·72 mm; height 0·32 mm; left valve: length 0·72 mm; height 0·32 mm. *Type locality:* Stat. 233 B, Inland Sea of Japan, 15 fathoms. (34°18′0″N, 133°35′0″E, trawled, 15 fathoms, blue mud, surface temp. 66·3°F, May 26, 1875.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 5, fig. 5. *Hinge* gonglyodont. *Central muscle scars:* adductor muscle scars consist of four vertically arranged central scars.

REMARKS. *Topotypic material:* a right valve, BM 1974.292.

Cythere arata Brady

(Pl. 16, figs 9–10; Fig. 2)

Cythere arata Brady, 1880 : 101, pl. 24, figs 2a–c.

LECTOTYPE. Right valve of penultimate instar, BM 80.38.52; designation by Benson (1972, p. 34, pl. 11, figs 16, 17). Length 0·96 mm; height 0·53 mm. *Type locality:* Stat. 167, west of New Zealand, 150 fathoms. (39°32′0″S, 171°48′0″E, trawled, blue mud, surface temp. 58·5°F, June 24, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 16, fig. 10. *Inner lamella:* anterior and posterior vestibula present but poorly developed. The posterior vestibule is as wide as the anterior one but not as long. The limits of the anterior vestibule are not defined. *Marginal pore canals:* posterior end has several canals whose endings are indistinct. Anteriorly, the canals are more evenly spaced, but more obscure; this is particularly true on the ventral side where their vague image can be seen along the edge. *Central muscle scars:* a vertical row of four and frontal scar (see Fig. 2). *Hinge* highly modified, antimerodont type; the anterior crenulate tooth is present. The median groove is only slightly crenulate, a slightly raised area with two points on the ends exists in the middle of the groove. The posterior tooth is smaller than the anterior tooth and is slightly crenulate.

REMARKS. *Cythere arata* Brady is the type species of *Bradleya*, Hornibrook, 1952.

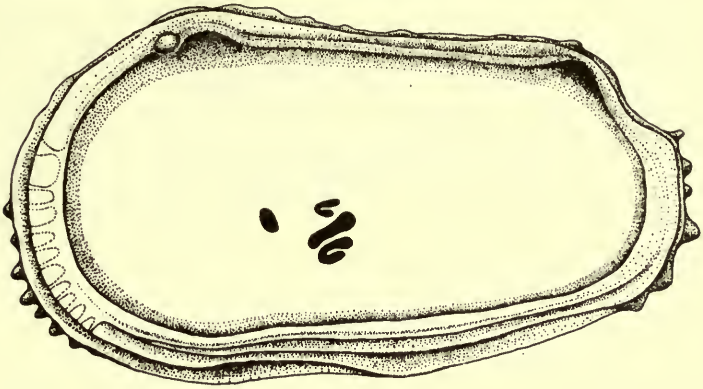


FIG. 2. *Cythere arata* Brady: interior view of lectotype (× 92).

Cythere bicarinata Brady

(Pl. 10, figs 12, 13)

Cythere bicarinata Brady, 1880: 70, pl. 16, figs 6a–d.

LECTOTYPE. Whole carapace, BM 80.38.50. Right valve: length 0·63 mm; height 0·27 mm; left valve: length 0·63 mm; height 0·28 mm. *Type locality:* Stat. 233 B, Inland Sea of Japan, 15 fathoms. (34°20′0″N, 133°35′0″E, trawled, 15 fathoms, blue mud, surface temp. 66·3°F, May 26, 1875.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 10, figs 12 and 13.

REMARKS. *Topotypic material:* a left valve, BM 1974.282, and a right valve, BM 1974.281.

Cythere circumdentata Brady

(Pl. 17, figs 3–6; Fig. 3)

Cythere circumdentata Brady, 1880: 106, pl. 26, figs 2a–c.

LECTOTYPE. Left valve, probably a penultimate stage, BM 80.38.58. Length 1·21 mm; height 0·68 mm. *Type locality:* Stat. 276, off the northwestern end of the Tuamotu Archipelago, 2350 fathoms. (13°28′0″S, 149°30′0″W, trawled, red clay, bottom temp. 35·1°F, surface temp. 80°F, September 16, 1875.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Inner lamella:* two vestibula of which the anterior vestibule is the larger. *Marginal pore canals:* only one straight and unbranched canal visible in the anterior region. *Hinge* amphidont, see Fig. 3. *Normal pores* scattered over the surface with more in the anterior and central regions. Most of the pores appeared to be open but several show resemblance to a sieve type. *Central muscle scars:* four vertically arranged adductor scars of which the uppermost scar is rather obscure. The dorsal

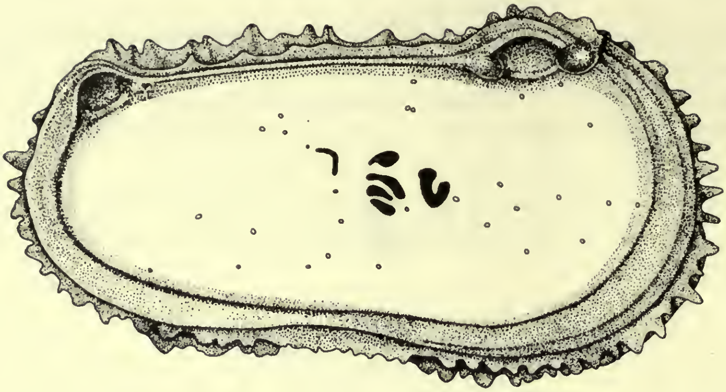


FIG. 3. *Cythere circumdentata* Brady : interior view of lectotype (× 73).

middle scar is flattened U-shape with the largest end extending over the scars beneath. Frontal scar V-shaped. A small dumb-bell shaped scar in the dorsal muscle scar field is present behind the adductor scars (see Fig. 3).

Cythere clavigera **Brady**

(Pl. 16, figs 1, 2 ; Fig. 4)

Cythere clavigera Brady, 1880 : 109, 110, pl. 23, figs 7a–d.

LECTOTYPE. Right valve (moult), BM 80.38.59. Length 0·90 mm ; height 0·47 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Inner lamella:* the area is so restricted in width that vestibula are non-existent. *Marginal pore canals:* none observed. *Hinge* modified between the antimerodont and hemimerodont types ; the anterior end consists of a flat, smooth tooth which is somewhat

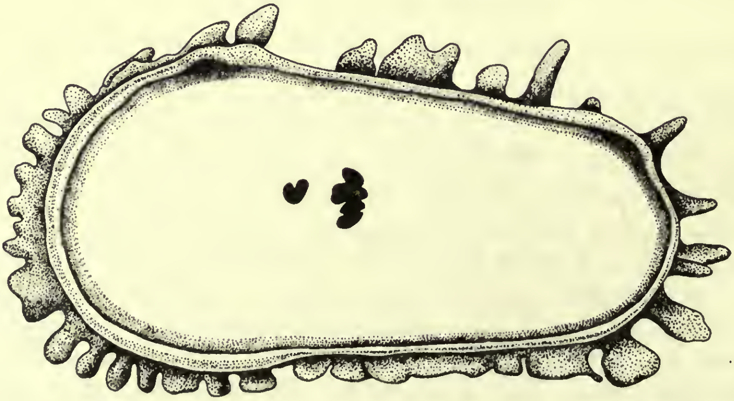


FIG. 4. *Cythere clavigera* Brady : interior view of lectotype (× 92).

rounded and has a very slight crenulation on the right valve. See Fig. 4. *Normal pores:* several apparent sieve types. *Central muscle scars:* adductor muscle scars four in number with the two bottom scars fused into one; the middle scar is square on one end and is larger than the rest. The frontal scar is V-shaped, partially obscured by the base of the external protuberance. There are two round scars in the dorsal area and a slight depression below the eye spot area of the side. See Fig. 4. *Eyespot* prominent.

Cythere craticula Brady

(Pl. 14, figs 9–12)

Cythere craticula Brady, 1880: 89, pl. 21, figs 7a–d.

LECTOTYPE. Left valve, BM 81.5.16. Length 0·74 mm; height 0·34 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 14, figs 9 and 10. *Marginal pore canals:* both anterior and posterior ends have numerous mostly straight pores; a few false pore canals are present. At the anterior margin one canal is branched and a few are curved. *Hinge* holamphidont. See Pl. 14, fig. 11. *Eyespots* present, but not well developed.

Cythere cristatella Brady

(Pl. 26, figs 5 and 7)

Cythere cristatella Brady, 1880: 90, pl. 19, figs 6a–d.

LECTOTYPE. Complete carapace, BM 80.38.63. Length 0·65 mm; height 0·37 mm. *Type locality:* Stat. 187, off Booby Island, 6–8 fathoms.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). See Pl. 26, figs 5 and 7.

REMARKS. Brady (1880, p. 90) described this species from only one locality (Stat. 187). Of several specimens present in sediment sample M-242, two are figured on Pl. 26, figs 5 and 7. *Topotypic material:* two complete carapaces, BM 1974.184–5.

Cythere cumulus Brady

(Pl. 6, figs 13–18; Pl. 7, fig. 5; Fig. 5)

Cythere cumulus Brady, 1880: 71, pl. 13, figs 2a–d.

LECTOTYPE. Disarticulated left and right valves, BM 81.5.17 (separated after photography). Right valve: length 0·50 mm; height 0·28 mm; left valve: length 0·50 mm; height 0·28 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

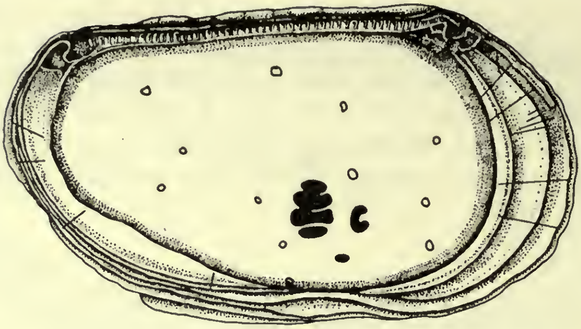


FIG. 5. *Cythere cumulus* Brady : interior (disarticulated) left valve view of lectotype (× 150).

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 6, figs 13, 14 and 17. *Inner lamella:* anterior vestibule much wider than posterior vestibule present only on the lower half of the posterior end. *Marginal pore canals* few, straight to slightly curved, widely spaced anterior and posterior marginal pore canals. See Pl. 6, figs 16 and 17 and Fig. 5. *Hinge* gongylodont. See Pl. 6, figs 16 and 18 and Fig. 5. *Normal pores* of sieve type with two configurations ; the more regular pore type and pores which seem to be linear openings in the sieve. *Central muscle scars:* adductor muscle scars, four, elongated, closely stacked, forming a crescent-shaped outline. A frontal scar is present in a somewhat flattened area (see Fig. 5).

REMARKS. Sediment sample M-198 (Port Jackson, Australia, 2–10 fathoms) yielded several specimens of this species. *Topotypic material:* a complete carapace, a right valve and two left valves, BM 1974.343–46.

Cythere curvicostata Brady

(Pl. 5, figs 16–19)

Cythere curvicostata Brady, 1880 : 84, 85, pl. 12, figs 4a–d.

LECTOTYPE. Whole carapace, BM 80.38.64. Length 0·59 mm ; height 0·34 mm. *Type locality:* Stat. 187, off Booby Island, 6 fathoms. (10°36′0″S, 141°55′0″E, dredged, coral sand, surface temp. 77·7°F, September 9, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Hinge* holamphidont.

Cythere cytheropteroides Brady

(Pl. 9, figs 5–8)

Cythere cytheropteroides Brady, 1880 : 78, pl. 15, figs 5a–d.

LECTOTYPE. Right valve, BM 80.38.67. Length 0·89 mm ; height 0·56 mm. *Type locality:* Stat. 142, off Cape of Good Hope, 150 fathoms. (35°04′0″S, 18°37′0″E dredged, sand, bottom temp. 47·0°F, surface temp. 65·5°F, December 18, 1873.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 9, figs 5 and 7. *Inner lamella:* the anterior and posterior vestibula are not well developed. *Hinge* hemiamphidont. See Pl. 9, figs 6 and 8. The anterior element is a worn tooth. Posterior tooth or lobe is broken and the median groove is worn so that crenulations cannot be seen. *Central muscle scars:* adductor muscle scars consist of four vertically stacked scars. One small V-shaped frontal scar is present.

REMARKS. A complete carapace and a right valve were found in sediment sample M-166 (Stat. 142). *Topotypic material:* a complete carapace and a right valve, BM 1974.333–4.

Cythere dasyderma Brady

(Pl. 11, figs 10, 11)

Cythere dasyderma Brady, 1880 : 105, 106, pl. 17, figs 4a–f ; pl. 18, figs 4a–f.

LECTOTYPE. Left valve (probably a penultimate stage), BM 1961.12.4.39. Length 1·20 mm ; height 0·71 mm. *Type locality:* Stat. 296. (38°6′0″S, 88°2′0″W, 1825 fathoms, bottom temp. 1·2°C, red clay, November 9, 1875.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880). *Hinge* holamphidont (imperfect). The anterior tooth and the anterior and posterior pits are not well developed. *Central muscle scars:* four adductor muscle scars are arranged vertically with a single frontal scar.

REMARKS. Brady described this species from 20 stations, including Stat. 296. The lectotype is from Stat. 296 and is probably a penultimate stage of left valve. A right valve was found in sediment sample M-237 (Stat. 185). Brady (1880) figured four complete carapaces, one from Stat. 317 (pl. 17, figs 4a–d) and the second from Stat. 122 (pl. 17, figs 4e, f) ; the third from Stat. 246 (pl. 18, figs 4a–d) and the fourth from Stat. 300 (pl. 18, figs 4e, f). *Topotypic material:* right valve, BM 1974.275 (Stat. 185, Torres' Straits, 155 fathoms, sand, August 31, 1874).

Cythere dictyon Brady

(Pl. 16, figs 6–8 ; Fig. 6)

Cythere dictyon Brady, 1880 : 99–101, pl. 24, figs 1a–y.

LECTOTYPE. Left valve, BM 1961.12.4.32 ; designation by Benson (1972, p. 36, pl. 11, fig. 18) ; see Fig. 6. Length 1·24 mm ; height 0·53 mm. *Type locality:* Stat. 78. (37°26′0″N, 25°13′0″W, dredged, 1000 fathoms, surface temp. 71·0°F, July 10, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Inner lamella:* both the anterior and posterior vestibula are well developed. *Marginal pore canals* numerous, unevenly spaced, bifurcated, trifurcated, and straight (see Fig. 6). *Hinge* holamphidont. The left valve with an anterior socket and tooth, a median, slightly crenulate bar and a posterior socket. See Fig. 6. *Normal pores* numerous, occupying positions in the centre of the reticulations. Some appear to be

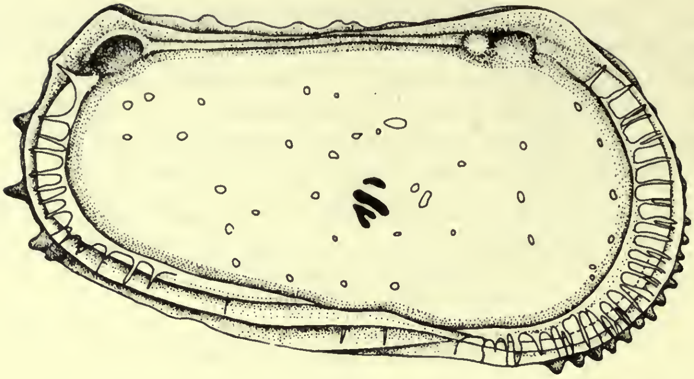


FIG. 6. *Cythere dictyon* Brady: interior view of lectotype (× 70).

sieve types but others are indefinite and may be open normal pores. *Central muscle scars:* the adductor muscle pattern consists of four scars vertically arranged. The lower two are fused to form a V-shaped scar. The ventral scar touches the middle scar, the dorsal scar is elongate and separated from the rest. The frontal scar is divided into separate scars, one circular and the other cylindrical in shape. There are two scars visible in the dorsal muscle field.

REMARKS. Humboldt Bay, Papua, 37 fathoms (M-277) is one of the many localities Brady (1880) reported this species to occur. Five specimens are from this station where the species is common. *Topotypic material:* a left valve, BM 1974.293, right valve, BM 1974.294, a left valve, BM 1974.295, a right valve, BM 1974.296, and a complete carapace, BM 1974.297.

Cythere dorsoserrata Brady

(Pl. 15, figs 1–4)

Cythere dorsoserrata Brady, 1880: 102, 103, pl. 23, figs 1a–d (*dorsiserrata* on pl. 23, figs 1a–d).

LECTOTYPE. Right valve, BM 81.5.19. Length 0·56 mm; height 0·47 mm. *Type locality:* Stat. 335, north of Tristan d'Acunha. (32°24′0″S, 13°5′0″W. 1425 fathoms, bottom temp. 2·3°C, *Globigerina* ooze, March 16, 1876.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880). *Inner lamella:* both the anterior and posterior vestibula are well developed. The anterior vestibule is long and narrow; the posterior one is shorter but its width gradually increases to a point where it is wider than the anterior vestibule. *Marginal pore canals:* the anterior pores are generally straight, a few are bifurcated. False pore canals are particularly numerous anteriorly; several straight canals are present but most are rather obscure. *Hinge* holamphidont. Right valve with a two-level cardinal tooth anteriorly, a mid-hinge groove that is coarsely crenulated anteriorly and changes at the mid-point and becomes smooth, and a posterior tooth which is broad, flat and smooth. *Central* *muscle scars:* the adductor muscles are placed vertically with two flat bars on the top, the bottom two are fused to form an upside-down triangle. The entire group has a forward slant. The frontal muscle scar is V-shaped with the top of the arms of the V poorly visible.

Cythere ericea Brady

(Pl. 10, figs 14–18)

Cythere ericea Brady, 1880 : 107, pl. 17, figs 1a–d.

LECTOTYPE. Right valve, BM 80.38.76. Length 1·13 mm ; height 0·71 mm. *Type locality:* Stat. 120, off Pernambuco. (8°37′0″S, 34°28′0″W, 675 fathoms, trawled, mud, surface temp. 28·0°F, September 9, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Inner lamella:* vestibula present at both anterior and posterior ends ; anterior vestibule larger than posterior one. *Marginal pore canals* straight, few and widely spaced. *Hinge* lophodont. Right valve with anterior and posterior tooth with slightly crenulated groove between. *Central muscle scars* very prominent with the adductor muscle consisting of four vertically arranged elongated scars with the dorsal scar slightly tipped away.

REMARKS. Brady (1880, p. 107) found this species at only one station (Stat. 120) and figured two left valves, one ornamented with spines (pl. 17, figs 1a–c) and the other denuded of spines (pl. 17, fig. 1d). Sediment sample M-140, which represents this station yielded a right valve. *Topotypic material:* a right valve, BM 1974.283.

Cythere exfoveolata Neviani

(Pl. 7, figs 16–19)

Cythere foveolata Brady, 1880 : 75, 76, pl. 13, figs 5a–h.
non *Cythere foveolata* Sequenza, 1880 : 324, pl. 17, fig. 23.
Cythere exfoveolata Neviani, 1928 : 106 (new name for *C. foveolata* Brady).

LECTOTYPE. Whole carapace, male, BM 80.38.81. Right valve: length 0·62 mm ; height 0·31 mm ; left valve : length 0·62 mm ; height 0·31 mm. *Type locality:* Stat. 51, off Heard Island, 75 fathoms. (52°59′30″S, 73°33′30″E, dredged, mud, surface temp. 36·2°F, February 7, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 7, figs 16, 17 and 19. *Eyespots* present, as upraised tubercles. *Inner lamella:* not observed. *Marginal pore canals:* none observed. *Hinge:* not observed.

REMARKS. Brady (1880, pp. 75, 76) reported this from two stations (Stat. 149 and 151) and figured complete carapaces of a female (pl. 13, figs 5a–d) and a male (pl. 13, figs 5e–h). The lectotype is from off Heard Island (Stat. 151) and a single left valve, which represents a female, was recovered from sediment sample M-185, which represents Stat. 151. *Topotypic material:* a left valve, BM 1974.288.

Cythere exilis Brady

(Pl. 10, figs 1–11)

Cythere exilis Brady, 1880 : 69, pl. 16, figs 5a–h.

LECTOTYPE. Disarticulated right and left valves, BM 81.5.20. Right valve : length 0·87 mm ; height 0·37 mm ; left valve : length 0·87 mm ; height 0·39 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 10, figs 1, 3. *Marginal pore canals* numerous, few curved, others straight. *Hinge* holamphidont, see Pl. 10, figs 9–11. *Normal pores* present, but type unclear. *Central muscle scars:* three adductor scars, one round frontal scar. *Overlap:* left valve is larger than the right valve.

REMARKS. Brady (1880, p. 69) found this species at only one station (Stat. 140) and figured a complete female carapace (pl. 16, figs 5a–d) and a male (pl. 16, figs e–h). A complete carapace, a right valve and a left valve (moult) were recovered from sediment sample M-164. *Topotypic material:* a complete carapace, BM 1974.278, a right valve, BM 1974.279, and a left valve, BM 1974.280.

Cythere falklandi Brady

(Pl. 6, figs 4–9)

Cythere falklandi Brady, 1880 : 65–66, pl. 12, figs 6a–f.

LECTOTYPE. Left valve, BM 80.38.78.A. Length 0·65 mm ; height 0·28 mm. *Type locality:* Stat. 316, Stanley Harbour, Falkland Islands, 6 fathoms. (51°32′0″S, 58°06′0″W, anchor mud, surface temp. 51·2°F, February 1, 1876.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). Inner *lamella:* the vestibule extends from the dorsal portion of the carapace near the anterior end of the hinge along the ventral edge narrowing at a point below the muscle scars and widening again as it follows through to the posterior end of the hinge. The anterior vestibule is wider than the posterior vestibule. *Marginal pore canals* few, straight, widely spaced. *Hinge* modified entomodont.

Cythere flabellicostata Brady

(Pl. 8, figs 1–4)

Cythere flabellicostata Brady, 1880 : 88, 89, pl. 13, figs 6a–h.

LECTOTYPE. Disarticulated left and right valves, BM 80.38.79. Right valve : length 0·75 mm ; height 0·37 mm ; left valve : length 0·75 mm ; height 0·37 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 8, figs 1–4. *Inner lamella:* the anterior and posterior vestibula are well developed with the former being the best developed. *Marginal pore canals* usually straight, although a few are branched, closely spaced, numerous marginal pore canals with a few false canals mostly at the posterior end. *Hinge* holamphidont (modified). Right valve in the anterior part has a tooth adjacent to a large antero-median socket, a corresponding tooth on the left valve. Posteriorly, the right valve has a lobed tooth. Left valve has a crenulated median bar. *Normal pores* of open type. *Overlap:* left valve larger than the right valve.

REMARKS. Brady (1880, pp. 88, 89) found this species only at Simon's Bay station and figured a complete female carapace (pl. 13, figs 6a–d) and a male carapace (pl. 13, figs 6e–j). Sediment sample M-164 yielded three valves, a male left and right valve and one female left valve. *Topotypic material:* a left valve, BM 1974.315, a right valve, BM 1974.316, and a left valve, BM 1974.317.

Cythere floscardui Brady

(Pl. 7, figs 1–4, 6, 7)

Cythere floscardui Brady, 1880 : 71, 72, pl. 13, figs 3a–h.

LECTOTYPE. Whole carapace, BM 80.38.80. Right valve: length 0·40 mm; height 0·25 mm; left valve: length 0·40 mm; height 0·25 mm. *Type locality:* Stat. 246, reefs off Honolulu, 40 fathoms, July 1875.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See also Pl. 7, figs 1, 3, 4, 7. *Central muscle scars:* see Pl. 7, fig. 2. *Eyespots* very slightly hyaline.

REMARKS. Brady (1880, pp. 71, 72) found this species occurring off reefs, Honolulu (Stat. 246). He figured a complete carapace of (?) female (pl. 13, figs 3a–d) and a (?) male (pl. 13, figs 4e–h). A female left valve recovered here from sediment sample M-324 (Stat. 246) where this species is common. *Topotypic material:* a female left valve, BM 1974.287.

Cythere fulvotincta Brady

(Pl. 8, figs 10–12)

Cythere fulvotincta Brady, 1880 : 67, pl. 14, figs 5a–d.

LECTOTYPE. Whole carapace, BM 81.5.21. Right valve: length 0·68 mm; height 0·37 mm; left valve: length 0·68 mm; height 0·37 mm. *Type locality:* Stanley Harbour, Falkland Islands, 6 fathoms.

DESCRIPTION. *Shape* as described by Brady (1880). *Ornamentation:* see Pl. 8, figs 10 and 12. *Eyespots* present but not well developed. *Overlap:* none.

Cythere hardingi nom. nov.

(Pl. 8, figs 8, 9)

Cythere ovalis Brady, 1880 : 66, 67, pl. 14, figs 4a–d.
non *Cythere ovalis* Stoddart, 1861 : 489, pl. 18, figs 5, 5A, 5B (Carboniferous, England).

LECTOTYPE. Whole carapace, BM 80.38.97. Right valve: length 0·74 mm; height 0·34 mm; left valve: length 0·74 mm; height 0·34 mm. *Type locality:* Stat. 187, off Booby Island, north of Australia, 6–8 fathoms. (10°36′0″S, 141° 55′0″E, dredged, coral and sand, surface temp. 77·7°F, September 9, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 8, fig. 8.

Cythere impluta Brady

(Pl. 9, figs 15, 16)

Cythere impluta Brady, 1880: 76, 77, pl. 16, figs 3a–d; pl. 26, figs 6a–d.

LECTOTYPE. Whole carapace (damaged), BM 1961.12.4.30. Right valve: length 0·73 mm; height 0·45 mm; left valve: length 0·74 mm; height 0·43 mm. *Type locality:* Stat. 316, Stanley Harbour, Falkland Island, 6 fathoms. February, 1876.

DESCRIPTION. *Shape and ornamentation:* See Brady (1880) and Pl. 9, figs 15 and 16.

Cythere inconspicua Brady

(Pl. 6, figs 10–12)

Cythere inconspicua Brady, 1880: 70, 71, pl. 13, figs 1a–d.

LECTOTYPE. Whole carapace, BM 81.5.22. Right valve: length 0·40 mm; height 0·22 mm; left valve: length 0·40 mm; height 0·21 mm. *Type locality:* Stat. 185, Torres' Straits, 155 fathoms. (11°35′25″S, 144°03′0″E, dredged, sand and shell, surface temp. 77·0°F, August 31, 1874.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880), and Pl. 6, figs 10 and 12.

REMARKS. Brady (1880, pp. 70, 71) found this species only at one station (Torres' Straits) and figured a complete carapace. A damaged left valve was recovered from sediment sample M-237, which represents Stat. 185. *Topotypic material:* a damaged left valve, BM 1974.286.

Cythere irpex Brady

(Pl. 11, figs 1–9)

Cythere irpex Brady, 1880: 107, pl. 17, figs 2a–d.

LECTOTYPE. Left valve, BM 80.38.86. Length 1·17 mm; height 0·71 mm. *Type locality:* Stat. 73, near Azores, 1000 fathoms. (38°30′0″N, 31°14′0″W, dredged, *Globigerina* ooze, bottom temp. 39·4°F, surface temp. 69·0°F, June 30, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 11, figs 1–4. *Inner lamella:* vestibula extremely narrow at both the anterior and posterior ends, the anterior vestibule being larger. *Marginal pore canals* numerous, straight, with a few false canals. *Hinge* holamphidont (modified). In the left valve, the hinge consists of an anterior socket, a tooth, a slightly crenulated bar, and a larger rounded socket. See Pl. 11, figs 6–9. *Central muscle scars:* see Pl. 11, fig. 5.

REMARKS. Brady (1880, p. 107) found this species at three stations (Stat. 73, 78, and 335). He figured a left valve (Brady 1880, pl. 17, figs 2a–d) ; the lectotype is a left valve from Stat. 73. A left and a right valve were recovered from sediment sample M-100. *Topotypic material:* a right valve, BM 1974.273, and a left valve, BM 1974.274.

Cythere irrorata Brady

(Pl. 11, figs 12–14)

Cythere irrorata Brady, 1880 : 108, 109, pl. 28, figs 2a–d.

LECTOTYPE. Whole carapace, BM 80.38.86A. Length 0·74 mm ; height 0·40 mm. *Type locality:* off Admiralty Island, 16–25 fathoms, March 7, 1875.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 11, figs 12–14.

Cythere kerguelenensis Brady

(Pl. 12, figs 14–18)

Cythere kerguelenensis Brady, 1880 : 78, 79, pl. 4, figs 16–18, pl. 20, figs 1a–f.

LECTOTYPE. Whole specimen, BM 80.38.88. Right valve : length 0·68 mm ; height 0·40 mm ; left valve : length 0·67 mm ; height 0·39 mm. *Type locality:* Stat. 162, off East Moncœur Island, Bass Strait, 38 fathoms. (39°10′30″S, 146°37′0″E, dredged, surface temp. 63·2°F, April 2, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 12, figs 14–18.

REMARKS. Brady (1880) reported this species from Balfour Bay (20–50 fathoms) ; Royal Sound, Kerguelen Island (28 fathoms) ; off Prince Edward's Island (50–150 fathoms) ; off East Moncœur Island (Stat. 162) and Port Jackson, Australia (2–10 fathoms). He figured a complete carapace of a female (pl. 20, figs 1a–c) and of a male (pl. 20, figs 1d–f). The lectotype is from Stat. 162. A right valve was recovered from M-195 (Stat. 162) and a complete carapace from sediment sample M-169 (off Prince Edward's Island, 50–150 fathoms). *Topotypic material:* a whole carapace, BM 1974.313, and a right valve, BM 1974.314.

Cythere* (?) *laganella Brady

(Pl. 27, figs 7–9)

Cythere (?) *laganella* Brady, 1880 : 63, pl. 16, figs 7a–d.

LECTOTYPE. Complete carapace, BM 81.5.23. Length 0·47 mm ; height 0·25 mm. *Type locality:* Stat. 185, Torres Straits, 155 fathoms. (11°35′0″S, 144°3′0″E, August 31, 1874.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880).

REMARKS. *Topotypic material:* a complete carapace, BM 1974.320.

Cythere lauta Brady

(Pl. 14, figs 5–8)

Cythere lauta Brady, 1880 : 85, pl. 21, figs 4a–d.

LECTOTYPE. Whole carapace, BM 81.5.24. Length 0·62 mm ; height 0·26 mm. *Type locality:* Stat. 187, off Booby Island, north of Australia. (10°36′0″S, 141°55′0″E, dredged, 6–8 fathoms, coral mud, surface temp. 77·7°F, September 9, 1874.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 14, figs 5–8. *Eyespots* well developed. Internal features not observed.

REMARKS. Brady (1880, p. 85) described this species from only one station (Stat. 187) and figured a complete carapace (pl. 21, figs 1a–d). Sediment sample M-242 yielded a left valve and a complete carapace. *Topotypic material:* a left valve, BM 1974.290, and a complete carapace, BM 1974.291.

Cythere lepralioides Brady

(Pl. 12, figs 10, 11)

Cythere lepralioides Brady, 1880 : 94, pl. 19, figs 5a–d.

LECTOTYPE. Right valve of a late instar, BM 80.38.91. Length 0·75 mm ; height 0·47 mm. *Type locality:* Stat. 142, off Cape of Good Hope, 150 fathoms. (35°04′0″S, 18°37′0″E, dredged, sand, bottom temp. 47·0°F, surface temp. 65·5°F, December 18, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 12, fig. 10. *Inner lamella:* the anterior vestibule is very small but the posterior vestibule is even smaller and narrower. *Hinge* lophodont. The hinge is not fully developed, but the anterior and posterior elements have a smooth broad tooth, each with a smooth groove. See Pl. 12, fig. 11. *Central muscle scars:* adductor muscle scar consists of four elongated scars vertically arranged.

REMARKS. Brady (1880, p. 94) reported this species from two stations (Simon's Bay, Stat. 140, and off Cape of Good Hope, Stat. 142) and he figured a complete carapace. The lectotype is a late instar of a right valve from Stat. 142. This species is common in Simon's Bay sediment sample M-164. *Topotypic material:* a right valve, BM 1974.312.

Cythere lubbockiana Brady

(Pl. 8, figs 13, 14)

Cythere lubbockiana Brady, 1880 : 68, 69, pl. 14, figs 6a–d.

LECTOTYPE. Whole carapace, BM 81.5.25. Left valve: length 0·81 mm; height 0·34 mm; right valve: length 0·79 mm; height 0·33 mm. *Type locality:* Stat. 187, Booby Island, north of Australia, 6–8 fathoms. (10°36′0″S, 141°55′0″E, dredged, coral and sand, surface temp. 77·7°F, September 9, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 8, fig. 13. *Overlap*, slight overlap of right valve by the left.

REMARKS. Brady (1880, pp. 68, 69) reported this species from only one station and he figured a complete carapace (pl. 14, figs 6a–d). Two specimens, one complete and the other a left valve, were recovered from sediment sample M-242, which represents this station. *Topotypic material:* a complete carapace, BM 1974.321, and a left valve, BM 1974.322.

Cythere mackenziei nom. nov.

(Pl. 9, figs 1–4)

Cythere pyriformis Brady, 1880 : 77, 78, pl. 15, figs 3a–d.
non *Cythere amygdaloides pyriformis* Cornuel, 1846 : 198, fig. 11 (Lower Cretaceous, France).

LECTOTYPE. Left valve, BM 80.38.103. Length 1·09 mm; height 0·68 mm. *Type locality:* Stat. 120, off Pernambuco, Brazil, 675 fathoms. (8°37′0″S, 34°28′0″W, trawled, mud, surface temp. 78·0°F, September 9, 1873.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880). *Inner lamella:* anterior vestibule very well developed. *Marginal pore canals* mostly straight, a few branched and many marginal pore canals present in the anterior and posterior vestibula. *Hinge* amphidont/heterodont. *Normal pores* open. *Central muscle scars:* the central muscle scars consist of four prominent, vertical, closely arranged adductor muscles and one V-shaped frontal scar. See Pl. 9, fig. 2. *Eyespot* present.

REMARKS. Brady (1880, pp. 77, 78) reported this species only from Stat. 120 and figured a left valve (pl. 20, figs 3a–d); the lectotype designated in this paper is also a left valve. A broken left valve was recovered from sediment sample M-140. *Topotypic material:* a broken left valve, BM 1974.332.

Cythere moseleyi Brady

(Pl. 6, figs 1–3)

Cythere moseleyi Brady, 1880 : 64, 65, pl. 12, figs 5a–f.

LECTOTYPE. Whole carapace (male), BM 80.38.93. Right valve: length 0·68 mm; height 0·33 mm; left valve: length 0·68 mm; height 0·34 mm. *Type* *locality:* Stat. 316. Stanley Harbour, Falkland Islands, 6 fathoms. (51°32′0″S, 58°06′0″W, anchor mud, February 1, 1876.)

Description. *Shape and ornamentation* as described by Brady (1880). *Inner lamella* well developed, as observed through the shell. *Hinge* modified entomodont. *Central muscle scars:* the adductor scars are vertically arranged.

Cythere murrayana Brady

(Pl. 9, figs 17–19)

Cythere murrayana Brady, 1880 : 69, 70, pl. 16, figs 4a–h.

Lectotype. Whole carapace, BM 80.38.94. Right valve: length 0·46 mm; height 0·25 mm; left valve: length 0·47 mm; height 0·25 mm. *Type locality:* Wellington Harbour, New Zealand. (Trawl-net at trawl, between June 24, and July 8, 1874.)

Description. *Shape and ornamentation* as described by Brady (1880).

Cythere obtusalata Brady

(Pl. 5, figs 10–12)

Cythere obtusalata Brady, 1880 : 91, pl. 12, figs 1a–c.

Lectotype. Right valve, BM 80.38.96. Length 0·64 mm; height 0·34 mm. *Type locality:* Stat. 162, off East Moncœur Island, Bass Straits, 38–40 fathoms. (39°10′30″S, 146°37′0″E, dredged, sand, surface temp. 63·2°F, April 2, 1874.)

Description. *Shape and ornamentation* as described by Brady (1880). See Pl. 5, figs 10 and 12. *Inner lamella* narrow, widest anteriorly; no vestibula present. *Marginal pore canals* straight, few, moderately spaced. *Hinge* holamphidont, see Pl. 5, fig. 11. *Central muscle scars:* see Pl. 5, fig. 12.

Remarks. Brady (1880, p. 91) described this species from Stat. 162 and off Admiralty Islands. The lectotype is a right valve from Stat. 162 (Brady, 1880, pl. 12, figs 1a–c also figured a right). Two specimens, a right and a left valve, were recovered from sediment sample M-195 (Stat. 162). *Topotypic material:* a right valve, BM 1974.330, and a left valve, BM 1974.331.

Cythere packardi Brady

(Pl. 12, figs 4–6)

Cythere packardi Brady, 1880 : 88, pl. 19, figs 2a–d.

Lectotype. Whole carapace, BM 81.5.26. Left valve: length 0·56 mm; height 0·33 mm; right valve: length 0·54 mm; height 0·31 mm. *Type locality:* Stat. 187, Booby Island, north of Australia, 6–8 fathoms. (10°36′0″S, 141°55′0″E, dredged, coral and sand, surface temp. 77·7°F, September 9, 1874.)

Description. *Shape and ornamentation:* see Brady (1880), and Pl. 12, figs 4 and 6. *Eyespots:* a small eyespot is present.

Remarks. Brady (1880, p. 88) reported this species from only one station (off Booby Island) and he figured a complete carapace (pl. 9, figs 3a–d). A left valve was recovered from sediment sample M-242, which represents this station. *Topotypic material:* a left valve, BM 1974.311.

Cythere papuensis Brady

(Pl. 16, figs 11–18 ; Fig. 7)

Cythere papuensis Brady, 1880 : 95, pl. 25, figs 5a–d.

Lectotype. Left valve, BM 80.38.98. Length 0·78 mm ; height 0·48 mm. *Type locality:* Humboldt Bay, Papua, 37 fathoms, March 24, 1875.

Description. *Shape and ornamentation* as described by Brady (1880). See Pl. 16, figs 11, 12, 17. *Marginal pore canals:* the posterior pore canals are straight, some angled, and are mostly obscured except for two canals. Anterior pore canals are moderately numerous, straight and some are at an angle toward the dorsum. (See Fig. 7.) *Hinge* holamphidont (modified). See Pl. 16, figs 15, 16, 18 and Fig. 7. *Normal pores:* the open normal pores are numerous, usually one or two per reticulation on the carapace. *Central muscle scars:* the adductor muscle consists of four scars ; the middle dorsal scar resembles a down-facing, partially flattened L, the bottom two scars are very close together with the ventral-most scar being slightly anterior. The frontal scar is a somewhat, flattened V whose apex points to the bottom of the adductor muscle. In the dorsal scar field, one scar is visible directly above the gap between the adductor scars and the frontal scar (see Pl. 16, fig. 17 and Fig. 7).

Remarks. Brady (1880, p. 95) described and figured this species from only one station (Humboldt Bay, Papua). A right and a left valve were recovered from sediment sample M-277. *Topotypic material:* a right valve, BM 1974.298, and a left valve, BM 1974.299.

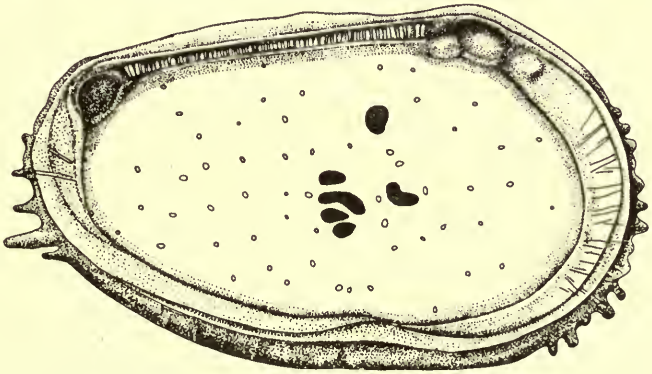


Fig. 7. *Cythere papuensis* Brady : interior view of lectotype (×97).

Cytheré parallelogramma Brady

(Pl. 8, figs 15–18)

Cythere parallelogramma Brady, 1880 : 82, 83, pl. 15, figs 1a–e.

Lectotype. Right valve, BM 80.38.99. Length 0·99 mm ; height 0·43 mm. *Type locality:* off Prince Edward's Island, 50–150 fathoms, December 26, 1874, near Stat. 145.

Description. *Shape and ornamentation* as described by Brady (1880), see Pl. 8, fig. 15. *Inner lamella:* anterior vestibule narrow. *Marginal pore canals* straight, evenly spaced and numerous. *Hinge* holamphidont (see Pl. 8, figs 16 and 18). *Central muscle scars:* central muscle scar area has a vertical adductor muscle pattern which consists of four scars, the second from the bottom is elongated into a dumb-bell shape and the top scar is divided into two with one V-shaped. The frontal muscle consists of three separate scars forming a V in outline. Three dorsal muscle scars are present (see Pl. 8, fig. 17).

Remarks. This species was reported by Brady (1880, pp. 82, 83) from only one station (off Prince Edward's Island) and he figured a male left valve (pl. 15, figs 1a–b) and a male right valve (pl. 15, figs 1c–e). A right and a left valve were recovered from sediment sample M-169, which represents this station. *Topotypic material:* a right valve, BM 1974.325, and a left valve, BM 1974.326.

Cythere patagoniensis Brady

(Pl. 15, figs 5–8)

Cythere patagoniensis Brady, 1880 : 93, pl. 23, figs 3a–d.

Lectotype. Whole carapace, BM 81.5.27. Right valve: length 0·68 mm ; height 0·38 mm ; left valve: length 0·71 mm ; height 0·38 mm. *Type locality:* Stat. 308, off Argentina, 175 fathoms. (50°08′30″S, 74°41′0″W, trawled, mud, surface temp. 51·7°F, January 5, 1876.)

Description. *Shape and ornamentation* as described by Brady (1880), see Pl. 15, figs 5 and 6. *Central muscle scars:* four vertically arranged adductor muscle scars, the top being separated, the next being the largest and slightly curved downward over the closely fitted ventral scars. Frontal scar is V-shaped. *Hinge* and details of *inner lamella* not observed.

Cythere quadriaculeata Brady

(Pl. 14, figs 14–18 ; Fig. 8)

Cythere quadriaculeata Brady, 1880 : 86, pl. 22, figs 2a–d, pl. 25, figs 4a–d.

Lectotype. Disarticulated right and left valves, BM 80.38.50. Right valve: length 0·52 mm ; height 0·34 mm ; left valve: length 0·53 mm ; height 0·34 mm.

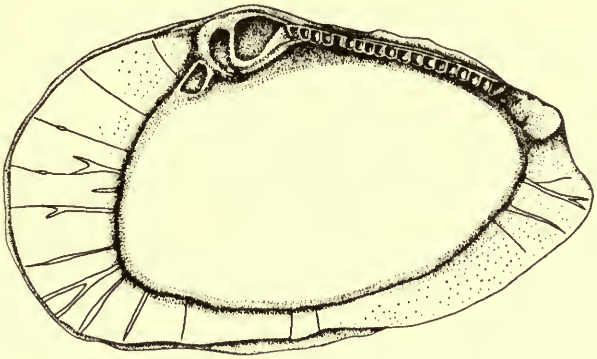


FIG. 8. *Cythere quadriculeata* Brady : interior (disarticulated) right valve view of lectotype (× 149).

Type locality: Stat. 233b, Inland Sea of Japan, 15 fathoms. (34°18′0″N, 133°35′0″E, trawled, mud, surface temp. 66·3°F, May 26, 1875.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 14, fig. 14. *Marginal pore canals* widely spaced, branching canals with a few false and straight canals. Some of the canals have a bulbous area midway along their length, see Fig. 8. *Hinge* holamphidont. See Pl. 14, figs 16 and 17 and Fig. 8. *Overlap:* left valve slightly larger than the right.

REMARKS. *Cythere quadriaculeata* Brady is the type species of *Spinileberis* Hanai, 1961. Brady (1880, p. 86) reported this species from two stations (Stat. 233b and off the reefs at Honolulu) and he figured a complete carapace from Honolulu Stat. (pl. 22, figs 2a–d) and another complete carapace from Stat. 233b (pl. 25, figs 4a–d). The lectotype is from the Inland Sea of Japan (Stat. 233b). A left valve recovered from sediment sample M-298 represents this station. *Topotypic material:* a left valve, BM 1974.329.

Cythere radula Brady

(Pl. 12, figs 7–9)

Cythere radula Brady, 1880 : 102, pl. 19, figs 4a, b.

LECTOTYPE. Left valve of a late instar, BM 81.5.28 ; designation by Benson (1972, p. 74, pl. 14, figs 16–18). Length 0·99 mm ; height 0·59 mm. *Type locality:* Stat. 191a, Ki Islands, southern Indonesia, 580 fathoms. (5°26′0″S, 133°19′0″E, mud, surface temp. 81·5°F, bottom temp. 40·7°F, September 24, 1874.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880), see Pl. 12, fig. 8. *Inner lamella:* very narrow anterior and the posterior vestibula present. *Hinge* holamphidont. *Central muscle scars:* the adductor muscle scars are four in number, vertically arranged, elongate and positioned on the posterior rim of the subcentral tubercle. The V-shaped frontal scar is positioned in the subcentral tubercle.

Cythere rastromarginata Brady

(Pl. 9, figs 9–14)

Cythere rastromarginata Brady, 1880 : 83, pl. 16, figs 1a–d, 2a–d.

Lectotype. Left valve, probably male, BM 80.38.105 ; designation by Benson (1972, p. 112, pl. 1, figs 1–4). Length 0·74 mm ; height 0·37 mm. *Type locality:* off reefs at Honolulu, 40 fathoms, July 1875.

Description. *Shape and ornamentation* as described by Brady (1880), see Pl. 9, figs 9, 10. *Marginal pore canals* straight, numerous, with a few branching canals present at both the anterior and posterior ends. See Pl. 9, fig. 13. *Hinge* holamphidont. *Central muscle scars:* adductor muscle scars consist of four vertically arranged scars, with a V-shaped frontal scar.

Remarks. *Cythere rastromarginata* Brady was selected type species of *Cletocythereis* by Swain, 1963. Brady (1880, p. 83) reported this species from three stations (off reefs, Honolulu ; Stat. 162 and Stat. 167) and he figured probable male (pl. 16, figs 1a–d) and female carapaces. The lectotype is a left valve, probably male, from reefs off Honolulu. Sediment sample M-324 which represents this station yielded three left valves. *Topotypic material:* three left valves, BM 1974.335–7.

Cythere sabulosa Brady

(Pl. 12, figs 1–3 ; Fig. 9)

Cythere sabulosa Brady, 1880 : 80, pl. 19, figs 1a–h (*fabulosa* on pl. 19).

Lectotype. Disarticulated right and left valves, BM 80.38.107. Right valve : length 0·68 mm ; height 0·40 mm ; left valve : length 0·68 mm ; height 0·40 mm.

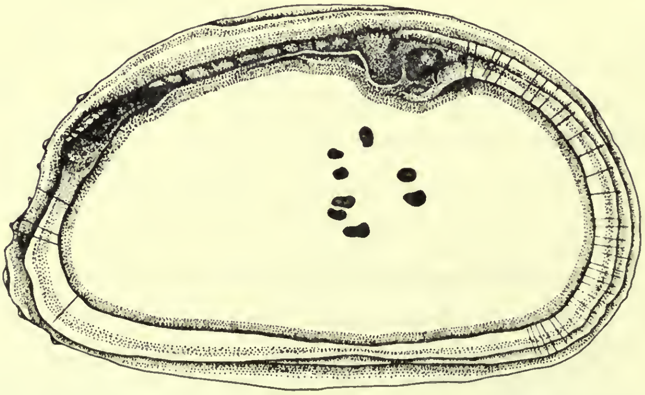


Fig. 9. *Cythere sabulosa* Brady : interior (disarticulated) left valve view of lectotype (×115).

Type locality: Stat. 187, Booby Island, north of Australia, 6–8 fathoms. (10°36′0″S, 141°55′0″E, dredged, coral and sand, surface temp. 77·7°F, September 9, 1874.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880), and Pl. 12, figs 1 and 2. *Marginal pore canals:* posterior margin has few pores. Anteriorly, the pore canals are most numerous on the ventral edge. Most are straight and moderately spaced. *Hinge* holamphidont (modified type). Anterior end of the right valve with a tooth pointed in front, flat and step-shaped behind. The median bar is smooth. The posterior element is a flat tooth. See Fig. 9. *Central muscle scars:* there is a widely spaced row of four adductor scars, second from the bottom split into two, a split frontal scar and a dorsal (?) fulcral scar; see Fig. 9. *Eyespots:* a simple, unstalked, definite eyespot is present.

REMARKS. Brady (1880, p. 80) reported this species from only one station (Booby Island) and figured a complete female carapace (pl. 19, figs 1a–d) and a complete male carapace (pl. 19, figs 1e–h). A female right and a female left valve were recovered from sediment sample M-242 where this species is common. *Topotypic material:* right and left valves, BM 1974.300–10.

Cythere scalaris Brady

(Pl. 14, fig. 13)

Cythere scalaris Brady, 1880 : 87, 88, pl. 21, figs 8a–c.

LECTOTYPE. Broken right valve (a moult with the centre portion missing), BM 80.38.109. Length 1·00 mm; height 0·53 mm. *Type locality:* Stat. 305, 100 fathoms, January 13, 1876.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Inner lamella:* the vestibula are nearly non-existent. *Marginal pore canals* not seen. *Hinge* of hemimerodont type (modified), the anterior element with a rather reduced broad crenulated tooth with the posterior having a similar, but slightly larger and more conspicuous tooth. The median area is a smooth groove. *Central muscle scars:* the carapace of the lectotype is broken in the muscle scar region.

REMARKS. Brady (1880, pp. 87, 88) reported this species from two stations (Stat. 185 and 305) and he figured a broken left valve (pl. 21, fig. 8a) and a broken right valve (pl. 21, figs 8b, c). The lectotype is a broken right valve from Stat. 305. A right and a left valve were recovered from sediment sample M-237, which represents Stat. 185. *Topotypic material:* a right and a left valve, BM 1974.327–8.

Cythere scintillulata Brady

(Pl. 8, figs 6, 7)

Cythere scintillulata Brady, 1880 : 62, 63, pl. 14, figs 3a–d.

LECTOTYPE. Whole carapace, BM 80.38.110. Right valve: length 0·68 mm; height 0·31 mm; left valve: length 0·68 mm; height 0·31 mm. *Type locality:*

Stat. 313, Straits of Magellan, 55 fathoms. (52°2′0″S, 6°0′0″W, trawled, sand, bottom temp. 57·8°F, surface temp. 48·2°F, January 20, 1876.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 8, fig. 6. *Inner lamella:* an anterior vestibule which is moderately wide is present in the paralectotype, BM 80.38.110. *Marginal pore canals:* few straight marginal pore canals present. *Central muscle scars* and *Hinge* not observed. *Normal pores* of open type.

REMARKS. Brady (1880, pp. 62, 63) reported this species from only one station (Straits of Magellan) and he figured a complete carapace (pl. 14, figs 3a–d) of a possible male. *Topotypic material:* two specimens, one a left valve, BM 1974.319, and the other a complete carapace of a probable female, BM 1974.318, were found in sediment sample M-369.

Cythere securifer Brady

(Pl. 7, figs 8–15)

Cythere securifer Brady, 1880 : 76, pl. 13, figs 4a–h.

LECTOTYPE. Left valve, BM 80.38.112. Length 0·59 mm; width 0·31 mm. *Type locality:* near Stat. 145, off Prince Edward's Island, 50–150 fathoms, December 26, 1874.

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 7, figs 8, 9, and 12. The apparent dimorphic posteroventral velate structures are shown on Pl. 7, figs 8–10. *Inner lamella:* the anterior vestibule is well developed and larger than the posterior vestibule which is widest on the dorsal side near the posterior hinge. *Marginal pore canals* straight, widely and regularly spaced. *Hinge* lophodont. see Pl. 7, figs 11, 14, and 15. *Central muscle scars:* adductor muscle scars consist of four elongate scars arranged vertically but forming a slanted group. A frontal scar is present but the rest are obscured by ornamentation. See Pl. 7, fig. 12.

Cythere* (?) *serratula Brady

(Pl. 24, figs 15, 16)

Cythere (?) *serratula* Brady, 1880 : 77, pl. 43, figs 7a–d.

LECTOTYPE. Right valve, BM 80.38.113, length 1·09 mm; height 0·62 mm, *Type locality:* Stat. 24, off Culebra Island, West Indies, 390 fathoms. (18°38′30″N. 65°05′30″W, dredged, coral mud, surface temp. 76·0°F, March 25, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 24, fig. 15. *Hinge:* undifferentiated type. Selvage forming valve edge. See Pl. 24, fig. 16. *Central muscle scars:* two curved parallel rows (Cytherellid type) with four and five scars respectively.

REMARKS. Brady (1880, p. 77) reported this species from Stat. 24, Stat. 85, and Stat. 335. The lectotype, a right valve, is from Stat. 24. *Topotypic material:* a left valve, BM 1974.387, was picked from sediment sample M-44 (Stat. 24). Two small specimens recovered from sediment sample M-106 (Stat. 85, off Canaries, 1125 fathoms) may belong to this species.

Cythere scabrocuneata Brady

(Pl. 26, figs 6 and 8)

Cythere scabrocuneata Brady, 1880 : 103, pl. 17, figs 5a–f ; pl. 23, figs 2a–c.
non *Trachyleberis scabrocuneata* (Brady), Brady, 1898 : 444, pl. 47, figs 1–7, 18–25.
non *Trachyleberis scabrocuneata* (Brady), Hornibrook, 1952 : 32–33, pl. 3, figs 38, 39, 48.

LECTOTYPE. BM 1952.12.10, 1, 2 (specimen lost) ; designation by Harding & Sylvester Bradley (1953 p. 12). *Type locality:* Stat. 233b, Inland Sea, Japan, 15 fathoms (34°20′0″N, 133°35′0″E).

DESCRIPTION. *Shape and ornamentation:* see Pl. 26, figs 6 and 8. *Hinge* holamphidont. *Normal pores* simple.

REMARKS. *Topotypic material:* two specimens, a right and a left valve, BM 1974.324, were found in sediment material from Stat. 233b. The left valve is figured (Pl. 26, figs 6 and 8).

Cythere squalidentata Brady

(Pl. 16, figs 3–5)

Cythere squalidentata Brady, 1880 : 110, pl. 23, figs 8a–d (*squabidentata* on pl. 23).

LECTOTYPE. Whole carapace (early instar), BM 81.5.29 ; designated by Benson (1971 p. 8, pl. 1, fig. 9 ; *nomen dubium*). Right valve : length 0·43 mm ; height 0·26 mm : left valve : length 0·43 mm ; height 0·25 mm. *Type locality:* Stat. 323, off the coast of Uruguay, 1900 fathoms. (35°39′0″S, 50°47′0″W, trawled, grey ooze, bottom temp. 33·1°F, surface temp. 73·5°F, February 28, 1876.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 16, figs 3 and 4. *Overlap:* none.

Cythere stolonifera Brady

(Pl. 14, fig. 4)

Cythere stolonifera Brady, 1880 : 89, pl. 21, figs 3a–d.

LECTOTYPE. Articulated carapace with the anterior end damaged, BM 80.38.115. Right valve : length 0·74 mm ; height 0·37 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 14, fig. 4.

Cythere subrufa Brady

(Pl. 13, figs 1–9)

Cythere subrufa Brady, 1880 : 81, pl. 20, figs 3a–f.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.117. Right valve : length 0·78 mm ; height 0·38 mm ; left valve : length 0·81 mm ; height 0·40 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen, 20–50 fathoms, January 1874.

DESCRIPTION. *Shape and ornamentation:* see Brady (1880) and Pl. 13, figs 1, 4 and 5. *Marginal pore canals:* posterior canals, few mostly straight. Anteriorly the canals are most numerous on the ventral edge of the vestibula. They are all straight with a few false canals present, more frequently on the ventral edge. *Hinge* hemiamphidont, see Pl. 13, figs 7 and 8. *Normal pores* of open type. *Central muscle scars:* see Pl. 13, fig. 9. *Eyespots* present but not greatly developed.

REMARKS. Brady (1880, p. 81) reported this species from two stations (Balfour Bay, Kerguelen Island, Stat. 149, and off Prince Edward's Island) and he figured a male (pl. 20, figs 3a–d) and a female (pl. 20, figs 3e, f). *Topotypic material:* a right, BM 1974.347, and a left valve, BM 1974.348, were recovered from sediment sample M-169 which represents Prince Edward's Island, 50–150 fathoms.

Cythere suhmi Brady

(Pl. 17, figs 7–12 ; Fig. 10)

Cythere suhmi Brady, 1880 : 106, 107, pl. 26, figs 3a–h.

LECTOTYPE. Disarticulated right and left valves, BM 80.30.119. Right valve : length 1·21 mm ; height 0·68 mm ; left valve : length 1·15 mm ; height 0·68 mm. *Type locality:* Stat. 241, northwest Pacific, 2300 fathoms. (35°41′0″N, 157°42′0″E, trawled, red clay, bottom temp. 35·1°F, surface temp. 69·2°F, June 23, 1875.)

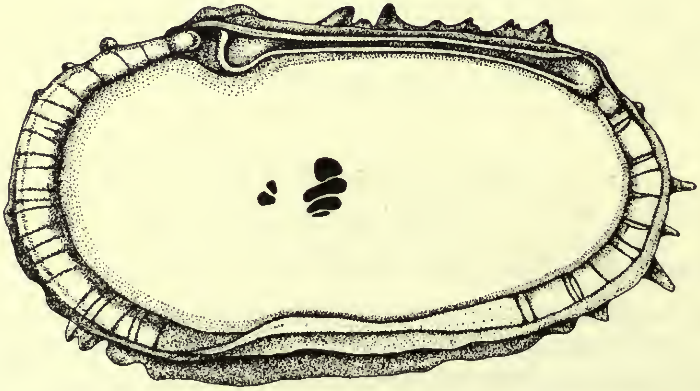


FIG. 10. *Cythere suhmi* Brady : interior view of lectotype (× 72).

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 17, figs 7, 8 and 10. *Inner lamella:* narrow anterior and posterior vestibula developed. *Marginal pore canals* more numerous at the anterior end; mostly straight with a few false canals. See Fig. 10. *Hinge* holamphidont. See Pl. 17, figs 9 and 10 and Fig. 10. *Central muscle scars:* adductor muscle scars four in number and arranged vertically. The two central scars are the larger and somewhat elongate. The dorsal scar is circular but faint, while the ventral scar is small and nearly fused with the one above. The frontal scar has two very close scars, one circular on the ventral side and one elongate on the more dorsal side; see Fig. 10.

REMARKS. Brady (1880, pp. 106, 107) reported this species from two stations (Prince Edward's Island and Stat. 241). He figured a female carapace (pl. 24, figs 3a–d) and a complete male (pl. 24, figs 3e–h). *Topotypic material:* a left valve, BM 1974.289, was recovered from sediment sample M-169 which represents Prince Edward's Island, 50–150 fathoms.

Cythere sulcatoperforata Brady

(Pl. 17, figs 1–2; Fig. 11)

Cythere sulcatoperforata Brady, 1880 : 99, pl. 26, figs 1a–d.

LECTOTYPE. Left valve, BM 81.5.30. Length 1·33 mm; height 0·81 mm. *Type locality:* Stat. 300, off Juan Fernandez Islands, west of Chile, 1375 fathoms. (33°42′0″S, 78°18′0″W, *Globigerina* ooze, trawled, bottom temp. 35·5°F, surface temp. 62·5°F, December 17, 1875.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 17, fig. 1. *Marginal pore canals:* the evidence of the canals is obscured and their width is very thin, straight and not bifurcated; see Fig. 11. *Hinge:* hemimerodont

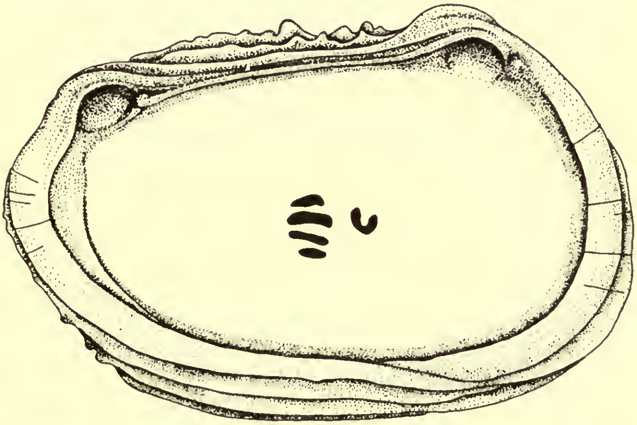


FIG. 11. *Cythere sulcatoperforata* Brady : interior view of lectotype (×62).

type: the left valve hinge consists of a broad anterior socket, a non-crenulate median bar, with a slight point two-thirds of the way back and a broad posterior socket, see Pl. 17, fig. 2, and Fig. 11. *Central muscle scars:* four oval adductor scars with a U-shaped frontal scar, see Pl. 17, fig. 2 and Fig. 11.

Cythere torresi Brady

(Pl. 12, figs 12, 13; Fig. 12)

Cythere torresi Brady, 1880: 67, 68, pl. 19, figs 8a–c (*torresii* on plate 19).

LECTOTYPE. Right valve, BM 81.5.31. Length 0·34 mm; height 0·22 mm. *Type locality:* Stat. 185, Torres Straits, 155 fathoms. (11°38′15″S, 143°59′38″E, dredged, sand and shells, surface temp. 77·0°F, August 31, 1874.)

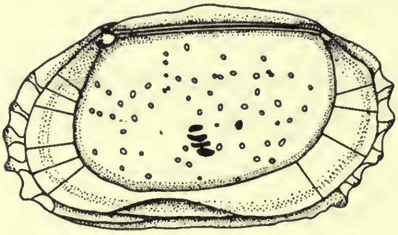


FIG. 12. *Cythere torresi* Brady: interior view of lectotype (× 150).

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 12 figs 12 and 13. *Inner lamella:* line of concrescence coincides with inner margin. *Marginal pore canals* few, widely spaced, mostly straight, one branched. There appears to be a number which are false but the determination is difficult because of the opaqueness of the inner lamella, see Fig. 12. *Hinge* between lophodont and antimerodont. The right valve has two terminal teeth that are very thin and appear crenulate. The groove is straight and gives the appearance of being slightly crenulate (see Fig. 12). *Normal pores* numerous and open; mostly terminally situated and not near the muscle scars or the valve edge. *Central muscle scars:* four prominent flattened scars. No frontal scars observed (see Fig. 12).

Cythere tricristata Brady

(Pl. 15, figs 17, 18)

Cythere tricristata Brady, 1880: 110, 111, pl. 23, figs 6a–d.

HOLOTYPE. Whole carapace, BM 80.38.121. Length 0·78 mm; height 0·37 mm. *Type locality:* off Admiralty Island, 16–25 fathoms, March 2, 1875.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 15, figs 17 and 18. *Hinge* holamphidont.

REMARKS. *Topotypic material:* a left valve, BM 1974.340, and two right valves, BM 1974.339 & 341.

Cythere tetrica Brady

(Pl. 27, figs 4–6)

Cythere tetrica Brady, 1880 : 104, pl. 23, figs 5a–d.

LECTOTYPE. Complete carapace, BM 80.38 (lost during photography). Length 0·54 mm ; height 0·27 mm. *Type locality:* Stat. 187, off Booby Island, lat. 10°36′0″S, long. 141°44′0″E, 6–8 fathoms.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880), see Pl. 27, figs 4–6.

REMARKS. The lectotype was lost during photography by R. H. Benson. *Topotypic material:* one complete carapace was recovered from sediment sample M-242, which represents Stat. 187 and is figured here (Pl. 27, figs 4–6). This specimen (BM 1974.338), a complete carapace, measures : length 0·64 mm ; height 0·32 mm.

Cythere velivola Brady

(Pl. 15, figs 9–16 ; Fig. 13)

Cythere velivola Brady, 1880 : 111, pl. 23, figs 4a–c.

LECTOTYPE. Left valve (moult), BM 80.38.122. Length 0·71 mm ; height 0·37 mm. *Type locality:* Stat. 189, Arafura Sea, 8 fathoms. (9°36′0″S, 137°50′0″E, trawled, mud, surface temp. 79·0°F, September 11, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 15, figs 9, 15 and 16. *Inner lamella:* extremely narrow posterior and anterior vestibula, almost non-existent (Pl. 15, fig. 12). *Marginal pore canals* straight to slightly curved, evenly spaced, bifurcating (one trifurcating) with several false canals. See Pl. 15, fig. 12, and Fig. 13. *Hinge* holamphidont, see Pl. 15, figs 13 and 14, and Fig. 13. *Normal pores* present over most of the surface and appear to be of sieve

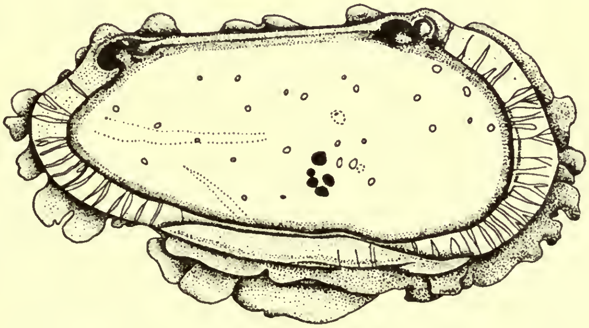


FIG. 13. *Cythere velivola* Brady : interior view of lectotype (×97).

type. *Central muscle scars:* adductor muscle scars a vertical row of four, the third scar from the dorsal side is divided into two ; frontal scar is made up of three scars in a horizontal line. A dorsal muscle scar is present above the adductor scars, see Fig. 13.

Cythere vellicata Brady

(Pl. 5, figs 13–15 ; Fig. 14)

Cythere vellicata Brady, 1880 : 64, pl. 12, figs 2a–d.

LECTOTYPE. Disarticulated left and right valves, BM 81.5.32 (separated after photography). Length 0·50 mm ; width 0·19 mm. *Type locality:* Port Jackson, depth 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 5, fig. 13. *Inner lamella:* anterior vestibule irregular in outline, posterior vestibule narrow (see Fig. 14). *Marginal pore canals* branching, anterior and posterior canals arising from very broad bases at the inner edge of the vestibule. *Hinge:* see Fig. 14. *Normal pores* clustered in the anterior half of the carapace. *Central muscle scars:* adductor muscle scar has three close, vertically stacked scars with a large kidney-shaped frontal scar.

REMARKS. *Topotypic material:* a complete carapace, BM 1974.365.

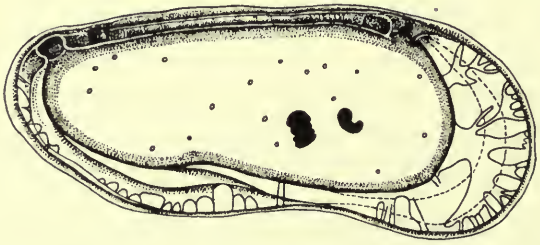


FIG. 14. *Cythere vellicata* Brady : interior (disarticulated) left valve view of lectotype (×142).

Cythere viminea Brady

(Pl. 11, fig. 15)

Cythere viminea Brady, 1880 : 94, pl. 18, figs 3a–c.

HOLOTYPE. Right valve, broken, BM 81.5.33 ; designation by Benson (1972, p. 50, pl. 11, fig. 15 ; *nomen dubium.*) Length 0·81 mm ; height 0·43 mm. *Type locality:* Stat. 146, deep-sea, east of Prince Edward's Island, 1375 fathoms. (46°46′0″S, 45°31′0″E, trawled, *Globigerina* ooze, bottom temp. 35·6°F, surface temp. 43°F, December 29, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). *Eyespots* well developed.

Cythere wyvillethomsoni Brady

(Pl. 13, figs 10–18 ; Pl. 14, figs 1–3)

Cythere wyvillethomsoni Brady, 1880 : 82, pl. 20, figs 4a–f.

LECTOTYPE. Disarticulated left and right valves, BM 80.38.123. Left valve : length 0·83 mm ; height 0·38 mm ; right valve : length 0·83 mm ; height 0·38 mm. *Type locality:* Christmas Harbour, Kerguelen Island, 20–50 fathoms (on slide) ; January 29, 1874. (Stat. 149 ; depth 120 fathoms on p. 17.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 13, figs 10 and 11. *Inner lamella:* both the anterior and the posterior vestibula are well developed with the anterior vestibule slightly larger. *Marginal pore canals* numerous on antero-ventral corner reducing in number towards dorsal corner. Mostly straight, a few branched and a few false. Posterior canals mostly straight and few in number, see Pl. 13, figs 12 and 15. *Hinge* holamphidont. *Normal pores* of open type. *Central muscle scars:* muscle scar pattern present not easily discerned. *Eyespots* present, but not well developed. *Second antenna:* see Pl. 13, fig. 18. Obtained from the lectotype. *Penis:* see Pl. 13, fig. 18. Obtained from the lectotype.

REMARKS. Brady (1880, p. 82) reported this species from Stat. 149, Balfour Bay, Stat. 150, 151 and questionably from Stat. 185. He figured a female carapace (pl. 20, figs 4a–d) and a male (pl. 20, figs 4e, f). *Topotypic material:* four specimens, BM 1974.349–52, of this species were recovered from sediment sample M-185 (Stat. 151).

Genus ***KRITHE***

Krithe hyalina Brady

(Pl. 18, figs 1, 2)

Krithe hyalina Brady, 1880 : 115, pl. 27, figs 3a–d.

LECTOTYPE. Whole carapace, BM 81.5.34. Length 0·59 mm ; height 0·31 mm. *Type locality:* Stat. 233b, Inland Sea, Japan, 15 fathoms. (34°18′0″N, 133°35′0″E, trawled, mud, surface temp. 66·3°F, May 26, 1875.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880) and see Pl. 18, fig. 1. *Hinge* adont.

Krithe producta Brady

(Pl. 17, figs 16–18)

Krithe producta Brady, 1880 : 114, 115, pl. 27, figs 1a–j.

LECTOTYPE. Whole carapace, BM 80.38.127. Length 0·84 mm ; height 0·47 mm. *Type locality:* Stat. 146, 1375 fathoms. (46°46′0″S, 45°31′0″E, trawled, *Globigerina* ooze, bottom temp. 35·6°F, surface temp. 43·0°F, December 29, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 17, fig. 18. *Hinge* adont. *Central muscle scars:* see Pl. 17, figs 16 and 17.

REMARKS. Brady (1880, pp. 114, 115) lists this species from seventeen stations ranging in depth from 50 to 1675 fathoms and considered it to be cosmopolitan. The lectotype is from Stat. 146, depth 1375 fathoms. *Krithe producta* is common in sediment sample M-169 (off Prince Edward's Island, 50–150 fathoms) and as a species should be split into several subspecies. *Topotypic material:* two left valves, BM 1974.353 & 355, and a right valve, BM 1974.354.

Krithe tumida Brady

(Pl. 18, figs 3–5)

Krithe tumida Brady, 1880 : 115, 116, pl. 27, figs 4a–d.

LECTOTYPE. Whole carapace, BM 81.5.36 (valves separated after photography). Length 0·62 mm ; height 0·37 mm. *Type locality:* Stat. 323. (35°39′0″S, 50°47′0″W, trawled, grey ooze, 1900 fathoms, bottom temp. 33·1°F, surface temp. 73·5°F, February 28, 1876.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1800). See Pl. 18, fig. 3. *Hinge* adont.

REMARKS. Brady (1880, pp. 115, 116) reported this species from Stat. 323 although he also lists (p. 13) *Krithe tumida* from Stat. 64 (35°35′0″N, 50°27′0″W, 2750 fathoms, grey ooze, June 20, 1873.) A left valve was recovered from sediment sample M-86 (Stat. 64) and is registered BM 1974.356.

Genus ***LOXOCONCHA***

Loxoconcha africana Brady

(Pl. 18, figs 13, 14)

Loxoconcha africana Brady, 1880 : 118, pl. 28, figs 3a–d.

LECTOTYPE. Disarticulated right and left valves, portion of anteroventral margin missing, BM 80.28.130. Right valve : length 0·59 mm ; height 0·40 mm ; left valve : length 0·59 mm ; height 0·37 mm. *Type locality:* St Vincent, Cape Verde, 1070–1150 fathoms, April 26, 1876.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880), except for absence of papillae on lectotype. See Pl. 18, fig. 13. *Inner lamella* narrow anteriorly and posteriorly with anterior and posteroventral vestibula. *Marginal pore canals:* about 17 simple canals. *Hinge:* aberrant amphidont type. In the right valve there is an anterior crescent-shaped socket within which there is a small tooth. The median element is crenulated. The posterior element consists of a divided tooth with a socket between. *Normal pores* large, scattered, round and elongate sieve-type. *Central muscle scars:* row of four adductor scars, single V-shaped frontal scar. *Eyespot* present.

Loxoconcha anomala Brady

(Pl. 18, figs 6–9)

Loxoconcha anomala Brady, 1880 : 123, pl. 27, figs 5a–d.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.132. Right valve : length 0·65 mm ; height 0·43 mm ; left valve : length 0·62 mm ; height 0·43 mm. *Type locality:* from reefs at Honolulu, 40 fathoms, July 1875.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). See Pl. 18, figs 6–9. *Inner lamella* wide throughout, line of concrescence and inner margin coincide ; no vestibula. *Marginal pore canals* about 22 branching, mostly bifurcate, a few trifurcate and single. *Hinge* adont. *Central muscle scars:* adductors consist of a vertical row of four elongate scars and a frontal scar. *Eyespot* present.

REMARKS. *Topotypic material:* one specimen, a left valve (lost) and a right valve, BM 1974.360, was found in sediment sample M-324 (reefs at Honolulu).

Loxoconcha australis Brady

(Pl. 18, figs 17, 18 ; Pl. 19, figs 1–4)

Loxoconcha australis Brady, 1880 : 119, 120, pl. 28, figs 5a–f ; pl. 29, figs 3a–d.

LECTOTYPE. Left valve, BM 80.38.133. Length 0·78 mm ; height 0·37 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). See Pl. 19, figs 2 and 4. *Inner lamella:* see Pl. 18, fig. 18 ; Pl. 19, figs 2 and 3, the anterior vestibule is present but posteroventral vestibule absent. Inner lamella of about uniform width, selvage strong. *Marginal pore canals:* nine anterior and six ventral and posterior simple, straight canals. See Pl. 19, fig. 3. *Hinge:* see Pl. 19, fig. 3, aberrant amphidont, anteriorly a strong tooth followed by a crenulate bar. Posteriorly a large crescent-shaped socket with weak tooth. *Normal pores* scattered, large, rounded, sieve-type pore canals. *Central muscle scars:* vertical rows of four adductors, frontal scar kidney-shaped. *Eyespot* present and located low on carapace.

REMARKS. Sediment sample M-242 (Stat. 187, off Booby Island, lat. 10°36′0″S, long. 141°5′0″E, 6–8 fathoms) yielded six complete carapaces, one of which was disarticulated. *Topotypic material:* disarticulated carapace, BM 1974.363.

Loxoconcha honoluliensis Brady

(Pl. 19, figs 5, 6)

Loxoconcha honoluliensis Brady, 1880 : 117, 118, pl. 28, figs 6a–f.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.136. Right valve : length 0·62 mm ; height 0·43 mm ; left valve : length 0·59 mm ; height 0·43 mm. *Type locality:* reefs off Honolulu, 40 fathoms, July 1875.

Description. *Shape and ornamentation* as given by Brady (1880). See Pl. 18, figs 5 and 6. Lectotype and topotype pitted. Opaque areas present over most of the valves. *Inner lamella* widest anteriorly and posteroventrally. Line of concrescence irregular and indistinct. *Marginal pore canals:* most of the branching type terminating in two, mostly three branches near the outer margin. Less than 30 canals somewhat evenly spaced throughout, a few false canals at the anterior end. *Hinge* adont. Right valve with a medium groove between two bars. Left valve with a median bar. *Normal pores:* sieve type, large and numerous. *Central muscle scars:* a vertical row of four elongate scars with the dorsal-most the longest and concave dorsally. Frontal scar V-shaped. *Eyespots* low and somewhat indistinct.

Remarks. Type locality for the lectotype, sediment sample M-324, yielded only two specimens, a right and a left valve. *Loxoconcha honoluliensis* was selected as type species of *Loxoconchella* by Triebel, 1954. *Topotypic material:* a right valve, BM 1974.361 ; a left valve lost.

Loxoconcha pumicosa Brady

(Pl. 18, figs 10–12)

Loxoconcha pumicosa Brady, 1880 : 118, 119, pl. 28, figs 2a–d.

Lectotype. Whole carapace, BM 81.5.37 (left valve lost after photography). Length 0·50 mm ; height 0·34 mm. *Type locality:* Nares' Harbour, Admiralty Islands, 16 fathoms, March 2, 1875.

Description. *Shape and ornamentation* as described by Brady (1880). See Pl. 18, figs 10 and 11. *Inner lamella* widest anteriorly, anterior and posteroventral vestibula present. Selvage strong. *Marginal pore canals* simple and straight. *Hinge :* aberrant amphidont hinge. Anteriorly, a crescent-shaped socket with a weak tooth followed by a crenulate bar. Posteriorly, a large crescent-shaped and incompletely divided tooth with a small socket inside the crescent. *Eyespot* present but inconspicuous.

Remarks. Two complete carapaces of this species were recovered from sediment sample M-279 (Nares' Harbour). Brady (1880, pp. 118, 119) also reported this species from off Booby Island (Stat. 187). *Topotypic material:* a complete carapace, BM 1974.359.

Loxoconcha subrhomboidea Brady

(Pl. 18, figs 15, 16)

Loxoconcha subrhomboidea Brady, 1880 : 121, pl. 28, figs 4a–d.

Lectotype. Whole carapace, Hancock Museum (left valve missing after photography). Length 0·37 mm ; height about 0·24 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October, 1873.

Description. *Shape* as given by Brady (1880) except that the posterior is more angular than rounded and the caudal process is present but weak (see Pl. 18, fig. 15).

Ornamentation as given by Brady (1880) plus a heavy ventral ridge and deep furrow (see Pl. 18, fig. 15). *Inner lamella:* anterior and posteroventral vestibula present. Well-developed posteroventral flange. *Marginal pore canals* simple and straight. *Hinge:* median element smooth. Posterior element comprises a large crescentic tooth which is incompletely divided, and a small socket inside the crescent. *Normal pores* few, large rounded sieve-type pores.

REMARKS. *Topotypic material:* a left valve, BM 1974.362, was recovered from sediment sample M-164 (Stat. 140, Simon's Bay), this is the only locality where Brady (1880, p. 121) found this species.

Genus ***XESTOLEBERIS***

Xestoleberis africana Brady

(Pl. 19, figs 15, 16)

Xestoleberis africana Brady, 1880 : 126, pl. 30, figs 4a–c.

LECTOTYPE. Disarticulated right and left valves. Portion of anteroventral region missing on left valve, BM 81.5.40 (valves separated after photography). Right valve: length 0·40 mm; height 0·31 mm; left valve: length 0·40 mm; height 0·28 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880) except for absence of papillae. *Inner lamella* widest anteriorly narrowing posteroventrally; anterior and posteroventral vestibula present. *Marginal pore canals* short, simple canals throughout. About 20 canals, anteriorly. *Hinge* merodont. Right valve with terminal crenulated teeth. Crenulations continue into groove for median bar of left valve. Median bar smooth. *Normal pores* large, of sieve type. *Central muscle scars:* four elongate adductor scars, others obscure. *Eyespot:* eyepit large and '*Xestoleberis* spot' small. The spot, located low, is short and semicircular in shape.

REMARKS. This species was reported by Brady (1880, p. 126) from only one station (Simon's Bay). *Topotypic material:* sediment sample M-164 (Stat. 140) yielded a single right valve, BM 1974.388.

Xestoleberis expansa Brady

(Pl. 19, figs 13, 14)

Xestoleberis expansa Brady, 1880 : 129, 130, pl. 30, figs 3a–d.

LECTOTYPE. Left valve, BM 81.5.41. Length 0·31 mm; height 0·19 mm. *Type locality:* Stat. 323, off Uruguay, 1900 fathoms. (35°39′0″S, 50°47′0″W, trawled, grey ooze, bottom temp. 33·1°F, surface temp. 73·5°F, February 28, 1876.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). The surface is extremely smooth and polished. *Hinge* merodont. *Central muscle scars* consist of four scars and a frontal scar. *Eyespot:* eyepit and '*Xestoleberis* spot' present.

REMARKS. Brady (1880, p. 129) found one specimen, a complete carapace, which he figured (pl. 30, figs 3a–d). The British Museum slide catalogued as BM 81.5.41 contained two specimens, a complete carapace figured here on Pl. 19, figs 13 and 14, which, unfortunately, is not a *Xestoleberis*. Consequently the other specimen, a left valve, is designated lectotype.

Xestoleberis foveolata Brady

(Pl. 19, figs 11, 12)

Xestoleberis foveolata Brady, 1880 : 130, pl. 30, figs 1a–g.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.141 (valves separated after photography). Right valve : length 0·54 mm ; height 0·37 mm ; left valve : length 0·54 mm ; height 0·40 mm. *Type locality:* Stat. 187, Booby Island, north of Australia, 6–8 fathoms. (10°36′0″S, 141°55′0″E, dredged, coral and sand, surface, temp. 77·7°F, September 9, 1874.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). See Pl. 19, fig. 11. *Inner lamella* widest anteriorly ; anterior and posteroventral vestibula present, the former is wider. *Marginal pore canals* simple, straight and short. Most numerous anteroventrally. *Hinge* merodont. Right valve with anterior and posterior crenulate teeth connected by a smooth ridge with a groove above. Left valve with smooth median bar and crenulate sockets joined by a narrow groove and above the latter, an accommodation groove. *Normal pores* large and open. *Central muscle scars:* four elongate adductor scars arranged vertically and a frontal scar. *Eyespots:* eyepit small and not visible externally. '*Xestoleberis* spot' long, slender and uniform in width. *Overlap:* left valve larger than right valve.

REMARKS. The type locality is Stat. 187 and topotypes have been recovered from sediment sample M-242 (Stat. 187). *Topotypic material:* two carapaces, a left and a right valve, BM 1974.364 and 366–8.

Xestoleberis granulosa Brady

(Pl. 19, figs 17, 18)

Xestoleberis granulosa Brady, 1880 : 125, 126, pl. 30, figs 5a–d.

LECTOTYPE. Disarticulated right and left valves, Hancock Museum (valves separated after photography). Right valve : length 0·61 mm ; height 0·33 mm ; left valve : length 0·63 mm ; height 0·35 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880), except for the absence of papillae. *Inner lamella* wide anteriorly, narrowing towards posterior. Lamella widest posteriorly in region of posteroventral vestibule. Anterior vestibule wider than posterior. Line of concrescence more irregular in anteroventral region, less irregular elsewhere. *Marginal pore canals* most numerous anteriorly, with about 35 simple canals and a few false canals. Concentrated anteroventrally, and less numerous ventrally and posteriorly. Some branching canals occur ventrally. *Hinge* merodont. Right valve with anterior and posterior crenulate teeth. Left valve with median bar. Bar as prominent as the teeth. *Normal pores* large and of sieve type. *Central muscle scars:* a vertical row of four elongate scars and a frontal scar. *Eyespot:* eyepit obscure. '*Xestoleberis* spot' large and about twice as long as wide. *Overlap:* left valve larger than right.

REMARKS. Brady (1880, pp. 125, 126) reported this species from only two localities (Stat. 162, East Moncœur Island, Bass' Strait, 38–40 fathoms, and Port Jackson). The lectotype is from Port Jackson and 10 complete carapaces and detached valves were recovered from sediment sample M-198 (Port Jackson). *Topotypic material:* a complete carapace, BM 1974.323, and a right valve, BM 1974.324.

Xestoleberis nana Brady

(Pl. 20, figs 14, 15)

Xestoleberis nana Brady, 1880 : 126, pl. 31, figs 5a–c.

LECTOTYPE. Right valve, BM 80.38.143. Length 0·43 mm; height 0·28 mm. *Type locality:* Stat. 172, off Nukualofa, Tongatabu, 18 fathoms. (20°58′0″S, 175°09′0″W, dredged, coral, surface temp. 75·0°F, July 22, 1874.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880), see Pl. 20, figs 14 and 15. *Inner lamella:* see Pl. 20, fig. 15. Widest anteriorly, vestibula present anteriorly and posteroventrally. *Marginal pore canals* short, simple and straight; about 30 anteriorly with most of them concentrated anteroventrally. *Hinge* merodont. Right valve with anterior and posterior crenulate teeth and median groove. *Normal pores* large and open. Many with a 'halo' around the pore on the surface. *Central muscle scars:* a vertical row of four adductor scars and additional scars. *Eyespot:* eyepit indistinct, '*Xestoleberis* spot' of two distinctly separate slender filaments, one below the other. Both slightly convex anteriorly.

Xestoleberis setigera Brady

(Pl. 20, figs 9–11)

Xestoleberis setigera Brady, 1880 : 125, pl. 31, figs 2a–d and figs 3a–c.

LECTOTYPE. Disarticulated right and left valves. Portion of ventral surface of right valve missing, BM 80.38.145 (valves separated after photography). Right valve: length 0·59 mm; height 0·31 mm; left valve: length 0·59 mm; height 0·25 mm. *Type locality:* off Prince Edward's Island, 50–150 fathoms. (46°48′0″S, 37°49′30″E, dredged, grey sand, surface temp. 41·0°F, December 26, 1873.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880), except for the papillae which are absent in the lectotype but are present in the topotype. *Inner* *lamella* widest anteriorly; anterior and ventral vestibula present with the former the larger. The ventral vestibule is very narrow and terminates at the postero-ventral corner. *Marginal pore canals* most abundant anteriorly with about 20 simple straight and short canals plus a few false canals anteroventrally. Ventral canals simple and straight. *Hinge* merodont. Right valve with anterior and posterior crenulate teeth, left valve with smooth median bar. *Normal pores* large and open. *Central muscle scars* consist of four scars, the uppermost in the shape of a wide and shallow U. Frontal scar heart-shaped. *Eyespot:* eyepit present, '*Xestoleberis* spot' club shaped. *Overlap:* left valve larger than right.

REMARKS. Brady (1880, p. 125) reported this species from three places (off Christmas Harbour, Kerguelen Island, 120 fathoms; the station from which he figured this species; Stat. 151 and off Prince Edward's Island). The lectotype is from Prince Edward's Island. *Topotypic material:* a complete carapace, BM 1974.369, from sediment sample M-169, Prince Edward's Island.

Xestoleberis tumefacta Brady

(Pl. 20, figs 12, 13; Pl. 26, figs 1–3)

Xestoleberis tumefacta Brady, 1880: 128, 129, pl. 31, figs 4a–d.

NEOTYPE. Complete carapace, BM 1974.370. Length 0·54 mm; height 0·33 mm. *Type locality:* Nares' Harbour, Admiralty Islands, 16 fathoms, March 2, 1875.

DESCRIPTION. *Shape* as described by Brady (1880). See Pl. 26, figs 1–3. *Ornamentation*, smooth, see Pl. 26, figs 1 and 2. *Inner lamella* wide throughout. *Hinge* merodont. *Eyespot:* external eyespot absent, but internal '*Xestoleberis* spot' is present.

REMARKS. Brady (1880, pp. 128, 129) apparently was dealing with two different forms; the form figured by him (pl. 31, figs 4a–d) is a true *Xestoleberis* but in his description he says, 'This has very much the general aspect of *Loxoconcha*'. The only specimen in the BM collection (BM 81.5.44) (see Pl. 20, figs 12 and 13) is a *Loxoconcha*, the specimen of *Xestoleberis* being lost. Brady found *Loxoconcha pumicosa* and *Xestoleberis tumefacta* only at Nares' Harbour (see p. 24) and several specimens of the only *Xestoleberis* present at this station were found in sediment sample M-279. One of these is here made neotype and figured (see Pl. 26, figs 1–3). *Topotypic material:* two right valves, BM 1974.371–2.

Xestoleberis variegata Brady

(Pl. 20, figs 16–18)

Xestoleberis variegata Brady, 1880: 129, pl. 31, figs 8a–g.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.146. Right valve: length 0·52 mm; height 0·37 mm; left valve: length 0·50 mm; height 0·34 mm.

Type locality: Stats 93, 94, off St Vincent, Cape Verde, 1070–1150 fathoms. (16°42′0″N, 25°12′0″W, mud, surface temp. 78·0°F, August 5, 1873.)

DESCRIPTION. *Shape* as given by Brady (1880) for the left valve, except for the absence of a ventral sinus; the right valve is characterised by a flat dorsal surface in the region of the median bar/groove and a truncated posterior end, especially the dorsal half. See Pl. 20, figs 16–18. *Ornamentation:* the lectotype has only two small opaque spots, both posteriorly rather than variegated all over as indicated by Brady (1880). *Inner lamella:* anterior and posteroventral vestibula present with the former the widest. *Marginal pore canals* simple, straight canals, in excess of 20 anteroventrally. Also, numerous ventrally, but decreasing in number posteriorly. Some false canals present. *Hinge* merodont. Right valve with anterior and posterior crenulate teeth. Left valve with median smooth bar. *Normal pores* large and open. *Central muscle scars:* a vertical row of four adductor scars; frontal scar kidney shaped. *Eyespot:* '*Xestoleberis* spot' long and of uniform width except at the dorsal tip where it is narrow. The spot has a coarse granular appearance. *Overlap:* left valve larger than right.

Genus ***CYTHERURA***

Cytherura clavata Brady

(Pl. 19, figs 7–10)

Cytherura clavata Brady, 1880: 133, pl. 29, figs 7a–d.

LECTOTYPE. Left valve, BM 80.38.148. Length 0·60 mm; height 0·29 mm. *Type locality:* Stat. 316, Stanley Harbour, Falkland Islands, 6 fathoms. (51°32′0″N, 58°06′0″W, dredged, 4 fathoms, mud, surface temp. 51·2°F, February 3, 1876.)

DESCRIPTION. *Shape and ornamentation:* see Brady (1880).

Cytherura clausi Brady

(Pl. 21, figs 9, 10)

Cytherura clausi Brady, 1880: 134, pl. 32, figs 8a–d.

LECTOTYPE. Left valve, BM 81.5.47. Length 0·49 mm; height 0·26 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

DESCRIPTION. *Shape and ornamentation* as given by Brady. Surface strongly reticulate. *Inner lamella* very wide anteriorly where the inner margin runs a normal course; very wide posteriorly where it forms a strong curve. *Normal pores* moderately small, numerous, open.

REMARKS. Brady's syntypes (BM 81.5.17 and BM 81.5.45) labelled '*Cytherura clausi*' really represent *C. mucronata* Brady. Several specimens of *C. clausi* Brady were found in sediment sample M-164. Hornibrook (1952, p. 51, pl. 15, figs 242–244) reported and figured *Cytherura clausi* Brady from New Zealand, conspecific with the form described here.

Cytherura costellata Brady
(Pl. 21, figs 7, 8)

Cytherura costellata Brady, 1880 : 134, pl. 32, figs 7a–d.

LECTOTYPE. Right valve, BM 80.38.149. Length 0·47 mm ; height 0·23 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island, 20–50 fathoms, mud, January 1874.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Cytherura cribrosa Brady
(Pl. 21, fig. 2)

Cytherura cribrosa Brady, 1880 : 132, pl. 32, figs 5a–d.

LECTOTYPE. Whole carapace, BM 80.38.150. Length 0·59 mm ; height 0·37 mm. *Type locality:* Stat. 305, 160 fathoms. (47°48′0″S, 74°46′0″W, trawled, mud, surface temp. 55·0°F, January 1, 1876.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Cytherura cryptifera Brady
(Pl. 21, fig. 1)

Cytherura cryptifera Brady, 1880 : 134, 135, pl. 32, figs 4a–c.

LECTOTYPE. Left valve (damaged) Hancock Museum. Length 0·40 mm ; height 0·22 mm. *Type locality:* Stat. 162, off East Moncœur Island, Bass Strait, 38–40 fathoms. (39°10′30″S, 146°37′0″E, dredged, sand, surface temp. 63·2°F, April 2, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Cytherura curvistriata Brady
(Pl. 21, fig. 13)

Cytherura curvistriata Brady, 1880 : 131, pl. 32, figs 10a–d.

LECTOTYPE. Whole carapace, BM 81.5.46. Length 0·37 mm ; height 0·21 mm. *Type locality:* Port Jackson, Australia, 2–10 fathoms, April 20, 1874.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Cytherura lilljeborgi Brady
(Pl. 21, figs 3–6)

Cytherura lilljeborgi Brady, 1880 : 132, 133, pl. 32, figs 6a–d.

LECTOTYPE. Whole carapace, BM 80.38.151. Length 0·43 mm ; height 0·25 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island, 20–50 fathoms, mud, January 1874.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Cytherura mucronata Brady

(Pl. 21, figs 11, 12)

Cytherura mucronata Brady, 1880 : 133, 134, pl. 32, figs 9a–d.

LECTOTYPE. Whole carapace, BM 81.5.45. Length 0·50 mm ; height 0·28 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 18, 1873.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 21, fig. 11.

REMARKS. Brady (1880, pp. 133, 134) described both *Cytherura mucronata* and *Cytherura clausi* from Stat. 140 (Simon's Bay). The lectotype of *C. mucronata* (BM 81.5.45) and syntype specimens labelled by Brady as '*C. clausi*' really represent *C. mucronata.* Several specimens of Brady's *C. clausi* were found in sediment sample M-164 (Stat. 140).

Genus ***CYTHEROPTERON***

Cytheropteron abyssorum Brady

(Pl. 23, fig. 8)

Cytheropteron abyssorum Brady, 1880 : 138, pl. 34, figs 3a–d.

LECTOTYPE. Whole carapace, BM 81.5.49. Length 0·37 mm ; width (from ala of right to ala of left valve) 0·50 mm. *Type locality:* Stat. 160, Southern Australian Basin, 2600 fathoms. (42°42′0″S, 134°10′0″E, trawled, red clay, bottom temp. 33·9°F, surface temp. 55·0°F, March 13, 1874.)

DESCRIPTION. *Shape:* a large portion of each valve is missing and no attempt was made to study the specimen in detail. The description given by Brady (1880) fits the lectotype.

Cytheropteron* (?) *angustatum Brady

(Pl. 23, figs 15–17)

Cytheropteron (?) *angustatum* Brady, 1880 : 137, pl. 34, figs 5a, b ('*angustum*' on explanation to pl. 34).

LECTOTYPE. Left valve, BM 80.38.152. Length 0·46 mm ; height 0·28 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island, 20–50 fathoms, mud, January 1874.

DESCRIPTION. *Shape* as given by Brady (1880), except that the entire dorsal margin slopes towards the posterior. See Pl. 23, figs 15 and 16. *Ornamentation* as given by Brady (1880). *Inner lamella* widest at anterior end. Line of concrescence and inner margin coincide throughout, no vestibule at either end. *Hinge* of *Infracytheropteron* type (holoperatodont). *Central muscle scars:* see Pl. 23, fig. 17.

REMARKS. Brady (1880, p. 137) reported this species from Stat. 149 (Balfour Bay) and Stat. 185 (Torres' Straits, 155 fathoms) and he figured a left valve (pl. 34, figs 5a, b). The lectotype is also a left valve from Stat. 149. *Topotypic material:* sediment sample M-237 (Stat. 185) yielded a single right valve, BM 1974.375.

Cytheropteron assimile Brady

(Pl. 23, figs 1–7)

Cytheropteron assimile Brady, 1880 : 138, 139, pl. 34, figs 2a–d.

LECTOTYPE. Whole carapace, BM 80.38.153. Length 0·70 mm ; height 0·42 mm. *Type locality:* Stat. 151, off Heard Island, 75 fathoms. (52°59′30″S, 73°33′30″E, dredged, mud, surface temp. 36·2°F, February 7, 1874.)

DESCRIPTION. *Shape* as described by Brady (1880), except for posterior portion of dorsal margin. See Pl. 23, fig. 1. *Ornamentation* as given by Brady (1880). *Inner lamella:* vestibule present at anterior end. Otherwise line of concrescence and inner margin coincide. *Marginal pore canals* few in number and most are simple. *Hinge* with only the terminal portions of the median element crenulate, see Pl. 23, figs 3–7. *Normal pores* open and scattered. *Central muscle scars:* four undivided adductors. Frontal scar single and V-shaped.

REMARKS. Brady (1880, pp. 138, 139) described this species from off Christmas Harbour (Stat. 149) and off Heard Island (Stat. 151). The lectotype is from Stat. 151. *Topotypic material:* this species is common in sediment sample M-183 (Stat. 149) and two right valves and a left valve are registered, BM 1974.376–8.

Cytheropteron fenestratum Brady

(Pl. 23, fig. 18 ; Pl. 24, figs 1–6)

Cytheropteron fenestratum Brady, 1880 : 139, 140, pl. 34, figs 6a–d.

LECTOTYPE. Right valve, BM 80.38.154–155. Length 0·93 mm ; height 0·56 mm. *Type locality:* Stat. 149, off Christmas Harbour, Kerguelen Island, 120 fathoms. (48°43′45″S, 69°6′15″E, dredged, mud, surface temp. 38·8–39·0°F, January 29, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), except that the ventral surface is not 'irregularly nodulated'. *Inner lamella:* see Pl. 23, fig. 18. Line of concrescence and inner margin coincide except anteriorly where a vestibule is present. *Marginal pore canals* numerous and mostly simple. *Hinge:* see Pl. 24, figs 5 and 6. Terminal elements lobed, groove of median element smooth. *Normal pores*, numerous, scattered and open. *Central muscle scars:* five adductor scars arranged in a vertical row ; middle three more elongate than the dorsal- or ventralmost scars. Single frontal scar.

REMARKS. Brady (1880, pp. 139, 140) reported this species from two stations (149 and 335). He figured a complete carapace (pl. 34, figs 6a–d). The lectotype is a right valve from Stat. 149. *Topotypic material:* sediment sample M-183 (Stat. 149, off Christmas Harbour) yielded a right valve, BM 1974.379.

Cytheropteron mucronalatum Brady

(Pl. 22, figs 14–18)

Cytheropteron mucronalatum Brady, 1880 : 140, 141, pl. 33, figs 8a–d.

LECTOTYPE. Left valve, BM 80.38.157. Length 1·30 mm ; height 0·84 mm. *Type locality:* Stat. 296, near the Chile Rise in the eastern Pacific, 1825 fathoms. (38°6′0″S, 88°2′0″W, trawled, *Globigerina* ooze, bottom temp. 35·3°F, surface temp. 59·8°F, November 9, 1875.)

DESCRIPTION. *Shape:* the lectotype differs from description of *C. mucronalatum* by Brady (1880) in the following ways : height is not equal to more than two-thirds of the length, anterior end scarcely dentate, posterior end devoid of spines, dorsum not broadly arched, see Pl. 22, figs 15 and 18. *Ornamentation:* the elevated ridge mentioned by Brady (1880) is practically absent anteriorly and does not terminate in a strong short spine on the lectotype. Right valve does show the spine. *Inner lamella:* line of concrescence and inner margin coincide, vestibula absent. *Marginal pore canals* few, mostly simple, few false. *Hinge:* median element smooth. *Normal pores*, scattered and open. *Central muscle scars:* see Pl. 22, figs 15 and 17.

REMARKS. Brady (1880, pp. 140, 141) described this species from Stats 70, 224, 246, 296, 300 and 302 and he figured a complete carapace (pl. 33, figs 8a–d). The lectotype is a right valve from Stat. 296. *Topotypic material:* sediment sample M-92 (Stat. 70, 38°25′0″N, 35°50′0″W, 1675 fathoms) yielded a single left valve, BM 1974.380.

Cytheropteron patagoniense Brady

(Pl. 22, figs 12, 13)

Cytheropteron patagoniense Brady, 1880 : 139, pl. 33, figs 7a–d.

LECTOTYPE. Left valve, eroded, BM 80.38.158. Length 0·56 mm ; height 0·37 mm. *Type locality:* Stat. 305, 160 fathoms. (47°48′0″S, 74°46′0″W, trawled, mud, surface temp. 55·0°F, January 1, 1876.)

DESCRIPTION. *Shape:* see Pl. 22, fig. 12. Exceptions to Brady's (1880) description include broadly rounded anterior, anterior half of dorsal margin regular and gently sloping, posterior half of dorsal margin steeply sloping. *Ornamentation:* the ridge mentioned by Brady is absent on the lectotype. A posterior dorsal knob is present at about the position where the ridge terminates on Brady's specimen. *Hinge:* median element smooth. *Central muscle scars:* four adductor scars with single kidney-shaped frontal scar.

Cytheropteron scaphoides Brady

(Pl. 21, figs 14–18)

Cytheropteron scaphoides Brady, 1880 : 136, pl. 33, figs 1a–d.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.159. Right valve : length 0·37 mm ; height 0·19 mm ; left valve : length 0·37 mm ; height 0·15 mm.

Type locality: Stat. 149, Balfour Bay, Kerguelen Island, 20–50 fathoms, mud, January 1874.

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880). *Inner lamella:* anterior and posterior vestibula present with the former the larger of the two. *Marginal pore canals* few and simple. *Hinge* as follows: in the larger right valve, the sequence of elements anterior to posterior is socket, wedge-shaped (in dorsal view) tooth, crenulate bar, rounded (in dorsal view) tooth, socket. In smaller left valve, crenulate groove, socket, wedge-shaped tooth. In both valves, the high point of the wedge is towards the anterior end. See Pl. 21, figs 17 and 18. *Central muscle scars:* adductor scars consist of four adjacent but distinct scars arranged in a vertical row. Frontal scar single somewhat circular and large. *Overlap:* right valve larger than left.

Cytheropteron wellingtoniense Brady

(Pl. 23, figs 9–14)

Cytheropteron wellingtoniense Brady, 1880: 136, 137, pl. 34, figs 4a–d.

LECTOTYPE. Right and left valves of a once articulated specimen, BM 80.38.160. Right valve: length 0·56 mm; height 0·34 mm. *Type locality:* Wellington Harbour, New Zealand, depth unknown.

DESCRIPTION. *Shape* essentially as given by Brady (1880). Notable exception is prominent indentation in dorso-anterior region. See Pl. 23, fig. 10. *Ornamentation* as given by Brady (1880). *Inner lamella:* anterior vestibule present. *Hinge:* see Pl. 23, figs 11–13; terminal and median element crenulate. *Central muscle scars:* see Pl. 23, fig. 14, frontal scar V-shaped.

Genus ***BYTHOCYTHERE***

Bythocythere arenacea Brady

(Pl. 22, figs 1–5)

Bythocythere arenacea Brady, 1880: 142, pl. 33, figs 3a–g (*arenosa* on pl. 19).

LECTOTYPE. Left valve, BM 81.5.50. Length 0·75 mm; height 0·37 mm. Tip of posterior caudal process broken off and missing. *Type locality:* Stat. 185, Torres' Straits, 155 fathoms. (11°35′0″S, 144°3′0″E, dredged, sand and shells, surface temp. 77·0°F, August 31, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880). See Pl. 22, fig. 1. *Inner lamella:* see Pl. 22, figs 2 and 3. Well defined anterior vestibule present. *Hinge:* see Pl. 22, figs 4 and 5. *Central muscle scars:* five, arcuate, vertically arranged, elongate adductor scars and two frontal scars.

REMARKS. Brady (1880, p. 142) found 'several examples' from Stat. 185 and figured (see pl. 33, fig. 3) complete carapaces of both a male and a female. *Topotypic material:* two specimens, both left valves, were found in sediment sample M-237; one left valve is registered BM 1974.382.

Bythocythere* (?) *exigua Brady

(Pl. 3, figs 6–10)

Bythocythere (?) *exigua* Brady, 1880 : 143, 144, pl. 6, figs 7a–d (*exigna* on pl. 6).

LECTOTYPE. Disarticulated right and left valves, BM 81.5.51. Right valve : length 0·50 mm ; height 0·28 mm ; left valve : length 0·50 mm ; height 0·28 mm. *Type locality:* Stat. 313, Straits of Magellan, 55 fathoms. (52°21′0″S, 68°0′0″W, trawled, sand, bottom temp. 47·8°F, surface temp. 48·2°F, January 20, 1876.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Bythocythere pumilio Brady

(Pl. 22, figs 6–8)

Bythocythere pumilio Brady, 1880 : 142, 143, pl. 33, figs 4a–d.

LECTOTYPE. Whole carapace, BM 81.5.52. Length 0·45 mm ; height 0·21 mm. *Type locality:* Stat. 149, Balfour Bay, Kerguelen Island, 20–50 fathoms, mud, January 1874.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

Bythocythere velifera Brady

(Pl. 22, figs 9–11 ; Pl. 27, fig. 3)

Bythocythere velifera Brady, 1880 : 143, pl. 33, figs 5a–c.

NEOTYPE. Left valve, BM 1974.381. Length 0·59 mm ; height 0·47 mm. *Type locality:* Stat. 185, Torres' Straits, 155 fathoms. (11°35′0″S, 144°3′0″E, dredged, sand and shells, surface temp. 77·0°F, August 31, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

REMARKS. The only specimen in the British Museum labelled *Bythocythere velifera* (BM 81.5.53) is a *Cytheropteron* (see Pl. 22, figs 9–11), one of the two velate *Bythocythere* specimens found at the type locality is designated neotype.

Genus ***PSEUDOCYTHERE***

Pseudocythere fuegiensis Brady

(Pl. 1, figs 9, 10)

Pseudocythere fuegiensis Brady, 1880 : 145, pl. 1, figs 7a–d.

HOLOTYPE. Right valve, BM 81.5.54. (This is the only specimen found by Brady and figured as 7a–c.) Length 1·18 mm ; height 0·50 mm. *Type locality:* Stat. 311, 245 fathoms. (52°51′0″S, 73°53′0″W, trawled, mud, bottom temp. 46·0°F, surface temp. 50·0°F, January 11, 1876.)

DESCRIPTION. *Shape and ornamentation* as given by Brady (1880), except that the longitudinal striae are present over the entire surface but stronger in the posterior half. *Inner lamella:* anterior and posteroventral vestibula present, see Pl. 1, fig. 9. *Marginal pore canals* straight and simple. Cluster of three near centre of caudal process. *Hinge* adont. *Central muscle scars:* see Pl. 1, fig. 10.

Genus *CYTHERIDEIS*

Cytherideis laevata Brady

(Pl. 2, fig. 18 ; Pl. 3, figs 1–5)

Cytherideis laevata Brady, 1880 : 146, 147, pl. 6, figs 5a–d ; pl. 35, figs 6a–d.

LECTOTYPE. Disarticulated right and left valves, BM 80.38.164. Right valve : length 0·88 mm ; height 0·34 mm ; left valve : length 0·90 mm ; height 0·34 mm. *Type locality:* Stat. 151, off Heard Island, 75 fathoms. (52°59′30″S, 73°33′30″E, dredged, mud, surface temp. 36·2°F, February 7, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 2, fig. 18. *Hinge* adont, see Pl. 3, fig. 3. *Central muscle scars:* see Pl. 3, fig. 2.

REMARKS. Brady (1880, pp. 146, 147) did not mention the frequency of this species and he figures two complete carapaces (pl. 6, fig. 5 ; pl. 35, fig. 6). *Topotypic material:* this species is a common form in the sediment sample M-185 and a right and a left valve are registered BM 1974.385–6.

Genus *XIPHICHILUS*

Xiphichilus (?) *arcuatus* Brady

(Pl. 24, figs 7, 8)

Xiphichilus (?) *arcuatus* Brady, 1880 : 148, 149, pl. 35, figs 2a–d.

LECTOTYPE. Disarticulated right and left valves, BM 81.5.55. Right valve : length 0·53 mm ; height 0·19 mm ; left valve : length 0·53 mm ; height 0·19 mm. *Type locality:* Stat. 174c, 610 fathoms. (19°07′50″S, 178°19′35″E, trawled, *Globigerina* ooze, bottom temp. 39·0°F, surface temp. 78·0°F, August 3, 1874.)

DESCRIPTION. *Shape:* the lectotype differs from the description by Brady (1880) in that the anterior end is more rounded, ventral margin slightly concave anteriorly and convex posteriorly. *Ornamentation:* entire surface with many small longitudinal ridges that follow the general curvature of the dorsum. Ridges can be seen with transmitted light. *Inner lamella* widest anteriorly where a vestibule is present. Elsewhere the line of concrescence and inner margin coincide. *Marginal pore canals* few, straight and mostly single. Few false canals ventrally. *Hinge* merodont-lophodont. Right valve with small, terminal teeth and a long groove between. Left valve with a long smooth median bar between terminal sockets, the posterior tooth is the largest. *Central muscle scars:* adductor scars consist of four closely adjacent scars.

Xiphichilus complanatus Brady

Xiphichilus complanatus Brady, 1880 : 148, pl. 35, figs 4a–d.

LECTOTYPE. Left valve, BM 81.5.56 [specimen lost]. *Type locality:* Stat. 149, off Christmas Harbour, Kerguelen Island, 120 fathoms, January 29, 1874.

DESCRIPTION. *Shape* as given by Brady (1880). *Inner lamella,* very wide anteriorly and posteriorly. *Hinge* adont. *Normal pores* frequent, open.

REMARKS. Brady described this species only from Stat. 149. Three specimens (one adult and two juveniles) were found in sediment sample M-183. *Topotypic material:* a complete carapace, BM 1974.253.

Genus ***POLYCOPE***

(?) ***Polycope cingulata*** Brady

(Pl. 26, fig. 4)

Polycope cingulata Brady, 1880 : 170, pl. 35, figs 7a–d.

MATERIAL. Complete carapace, BM 1974.384. Length 0·49 mm. *Type locality:* None. Brady (1880, p. 170) mentioned that there is no record of the locality in which the only specimen of this species was found.

REMARKS. A single complete, eroded carapace, which may represent *Polycope cingulata,* was found in sediment sample M-198 (which represents Challenger Stat. Port Jackson, Australia, 2–10 fathoms, April 20, 1874.) The only articulated specimen which was figured by Brady as 7a–d on pl. 35 was never deposited either in the British Museum (Natural History) or in the Hancock Museum (*fide* letter by Mrs O. Marshall, secretary to Mr A. M. Tynan, Curator, Hancock Museum, dated 24 July 1967 to H. S. Puri).

Polycope* (?) *favus Brady

(Pl. 24, fig. 9)

Polycope (?) *favus* Brady, 1880 : 170, pl. 36, figs 4a–b.

LECTOTYPE. Left valve, BM 81.5.64. Length 0·44 mm ; height 0·40 mm. *Type locality:* Stat. 185, Torres' Straits, 155 fathoms. (10°35′0″S, 144°03′0″E, dredged, sand and shells, surface temp. 77·0°F, August 31, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880).

REMARKS. Brady (1880, p. 170) found 'one or two' valves from Stat. 185, and he figured a left valve. *Topotypic material:* two valves, one broken, were found from sediment sample M-237. A left valve is registered BM 1974.383.

Genus ***CYTHERELLA***

Cytherella cribrosa Brady

(Pl. 17, fig. 13)

Cytherella cribrosa Brady, 1880 : 176, pl. 26, figs 5a–c.

LECTOTYPE. Left valve, BM 81.5.66. Length 0·62 mm ; height 0·34 mm. *Type locality:* Stat. 172, off Nuknalofa, Tongatabu, 18 fathoms. (20°58′0″S, 175°09′0″W, dredged, coral, mud, surface temp. 75·0°F, July 22, 1874.)

REMARKS. The form described and illustrated by Brady does not resemble the lectotype. Brady (1880, p. 176) observed that the 'surface of the shell is destitute of ridges or undulations, but marked with numerous rather large oblong excavations'. The left valve figured by him as figs 5a–c is not as long (0·49 mm) as the lectotype (0·62 mm) which is obviously a *Cytherelloidea.* We have designated this specimen the lectotype as it was the *only* specimen found in the collection labelled as '*Cytherella cribrosa*, No. 172, D.18, off Tongatabu'. This is the only species of *Cytherella* in the dredging at Stat. 172, and Brady found it only at its type locality.

Cytherella dromedaria Brady

(Pl. 24, fig. 14)

Cytherella dromedaria Brady, 1880 : 173, pl. 43, figs 6a–b.

LECTOTYPE. Left valve, BM 81.5.67. Length 0·77 mm ; height 0·47 mm. *Type locality:* Stat. 140, Simon's Bay, South Africa, 15–20 fathoms, October 1873.

REMARKS. Brady (1880, p. 173) described this species from Stat. 140 (Simon's Bay) and he figured a left valve (pl. 43, figs 6a–b). The lectotype is also a left valve from Simon's Bay. *Topotypic material:* sediment sample M-164 (Simon's Bay, Stat. 140) yielded a right valve and a left valve, BM 1974.357–8.

Cytherella irregularis Brady

(Pl. 24, fig. 10)

Cytherella irregularis Brady, 1880 : 178, pl. 43, figs 3a–c.

LECTOTYPE. Left valve (damaged), Hancock Museum. (Same specimen as illustrated by Brady, pl. 43, figs 3a–c, photographed on original museum slide as the specimen is too fragile to transfer.) Length 0·72 mm ; height 0·33 mm. *Type locality:* Stat. 33, off Bermuda, 435 fathoms. (32°21′30″N, 64°35′55″W, dredged, coral mud, surface temp. 68·0°F, April 4, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 24, fig. 10.

Cytherella lata Brady

(Pl. 24, figs 17, 18)

Cytherella lata Brady, 1880 : 173, pl. 44, figs 5a–e.

LECTOTYPE. Right valve, BM 80.38.172. Length 0·81 mm ; height 0·56 mm. *Type locality:* Stat. 75, off Azores, 450 fathoms. (38°38′0″N, 28°28′30″W, dredged, sand, surface temp. 70·0°F, July 2, 1873.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 24, fig. 17. *Central muscle scars:* two curved transverse rows of six and nine elongate scars respectively.

REMARKS. Brady (1880, p. 173) reported this species from the following stations : off Culebra Island, West Indies, 390 fathoms, mud (Stat. 24) ; off Azores, lat. 38°37′0″N, long. 28°30′0″W, 450 fathoms, sand (Stat. 75) ; off Pernambuco, lat. 8°37′0″S, long. 34°28′0″W, 675 fathoms, mud (Stat. 120) ; Torres' Straits, lat. 11°35′0″S, long. 144°03′0″E, 155 fathoms, sand (Stat. 185) ; off Ki Islands, 580 fathoms, lat. 5°26′0″S, long. 133°19′0″S, mud (Stat. 191a). The lectotype is from Stat. 75. *Topotypic material:* a left valve recovered from sediment sample M-237 (Stat. 185), BM 1974.389.

Cytherella latimarginata Brady

(Pl. 17, figs 14, 15)

Cytherella latimarginata Brady, 1880 : 178, 179, pl. 36, figs 7a–d.

NEOTYPE. Disarticulated left and right valves, BM 81.5.69. Right valve : length 0·41 mm ; height 0·28 mm ; left valve : length 0·41 mm ; height 0·25 mm. *Type locality:* Stat. 185, Torres' Straits, 155 fathoms. (11°35′0″S, 144°03′0″E, dredged, sand and shells, surface temp. 77·0°F, August 31, 1874.)

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 17, figs 14 and 15.

REMARKS. Specimens of this species were never deposited either in the British Museum (Natural History) or the Hancock Museum (letter by Mrs O. Marshall, secretary to Mr A. M. Tynan, Curator, Hancock Museum, dated 24 July 1967, to H. S. Puri) and have been lost. Sediment sample M-237 (Stat. 185) yielded a single articulated valve, which is designated as neotype.

Cytherella venusta Brady

(Pl. 24, figs 11–13)

Cytherella venusta Brady, 1880 : 176, pl. 43, figs 4a–d.

LECTOTYPE. Right valve, BM 80.38.180. Length 0·71 mm ; height 0·34 mm. *Type locality:* off reefs at Honolulu, 40 fathoms, July 1875.

DESCRIPTION. *Shape and ornamentation* as described by Brady (1880), see Pl. 24, figs 11 and 13. *Central muscle scars:* see Pl. 24, fig. 12.

REMARKS. Off reefs at Honolulu is the only locality where Brady (1880, p. 176) found this species. *Topotypic material:* sediment sample M-324, which represents the type locality, yielded a right and a left valve, which are designated topotypes BM 1974.390–1.

REFERENCES

BATE, R. H. 1963. The Ostracoda collected during the voyage of H.M.S. Challenger. *Micropaleontology* **9** : 79–84.

BENSON, R. H. 1971. A new Cenozoic deep-sea genus, *Abyssocythere* (Crustacea : Ostracoda . Trachyleberididae), with description of five new species. *Smithson, Contr. Paleobiol:* **7** : 1–25, 3 pls.

—— 1972. The *Bradleya* problem. With descriptions of two new psychrospheric ostracode genera, *Argenocythere* and *Poseidonamicus* (Ostracoda : Crustacea). *Smithson. Contr. Paleobiol.* **12** : 1–138, 14 pls, 67 figs.

BRADY, G. S. 1866. On new or imperfectly known species of marine Ostracoda. *Trans. zool. Soc. Lond.* **5** : 359–393, pls 57–62.

—— 1867–1871. In : *Les Fonds de la Mer*, vol. 1.

—— 1878. A monograph of the Ostracoda of the Antwerp Crag. *Trans. zool. Soc. Lond.* **10** (8) : 379–409, pls 62–69.

—— 1880. Report on the Ostracoda dredged by 'H.M.S. Challenger' during the years 1873–1876. *Rep. scient. Results Voy. Challenger* **1** (3) : 1–184, 44 pls.

—— 1898. On new or imperfectly known species of Ostracoda, chiefly from New Zealand. *Trans. zool. Soc. Lond.* **14** : 429–452, pls 43–47.

CORNUEL, J. 1846. Description des entomostraces fossils du terrain Crétace inférieur du Département de la Haute-Marne suivie d'indications sur les profondeurs de la mer qui a déposé ce terrain. *Mém. Soc. géol. Fr.* ser. 1, **1** (2) : 193–205, 7 pls.

HARDING, J. P. & SYLVESTER-BRADLEY, P. C. 1953. The ostracode genus *Trachyleberis*. *Bull. Br. Mus. nat. Hist.* (Zool.) **2** : 1–15, 2 pls.

HORNIBROOK, N. DE B. 1952. Tertiary and Recent marine Ostracoda of New Zealand. *Palaeont. Bull. Wellington,* **18** : 1082, pls 1–18.

NEVIANI, A. 1928. Ostracodi fossil d'Italia. 1. Vallebiaja (Calabriano). *Memorie Accad. pont. Nuovi Lincei* ser. 2, **11** : 1–120.

SEGUENZA, G. 1880. Le formazioni terziarie nella provincia di Reggio (Calabria). *Memorie Accad. pont. Nuovi Lincei* **6** : 3–443, pls 4–17, 2 maps.

STODDART, W. W. 1861. On a Microzoa bed in the Carboniferous limestone of Clifton, near Bristol. *Ann. Mag. nat. Hist.* ser. 3, **8** : 486–490.

SWAIN, F. M. 1963. Pleistocene Ostracoda from the Gubik Formation, Arctic coastal plain, Alaska. *J. Paleont.* **37** (4) : 798–834.

TIZARD, T. H., MOSELEY, H. N., BUCHANAN, J. Y. & MURRAY, J. 1885. Narrative of the cruise of '*H.M.S. Challenger*' with a general account of the scientific results of the expedition. *Rep. scient. Results Voy. Challenger.* Narrative **1** : 1–1110.

Dr Harbans S. Puri
Bureau of Geology
903 West Tennessee St
Tallahassee
Florida 32304
U.S.A.

Dr Neil C. Hulings
Faculty of Science
University of Jordan
Amman
Jordan

PLATE 2

Figs 1–4. *Bairdia villosa* Brady, lectotype, BM 80.38.44. 1. Exterior view of left valve (× 25), incident light. 2. Muscle scar of right valve (× 145). 3. Right valve, incident light. 4. Right valve, transmitted light.

Figs 5, 6. *Argilloecia eburnea* Brady, lectotype, BM 80.38.9. 5. Exterior view of left valve (× 60). 6. Enlargement of muscle scar pattern (× 260).

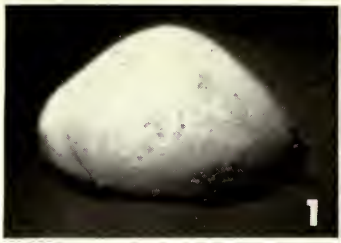
Figs 7–10. *Bythocypris reniformis* Brady, lectotype, BM 80.38.19. 7–8. Exterior views of right valve, incident and transmitted light (× 35). 9. Interior view of anteroventral portion of marginal area. 10. Muscle scars (both × 105), transmitted light.

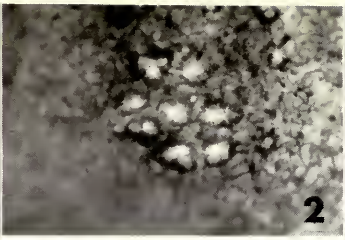
Figs 11, 12. *Bythocypris elongata* Brady, lectotype, BM 81.5.8. 11. External view of right valve (× 25). 12. Enlargement of muscle scar pattern of right valve (× 85), transmitted light.

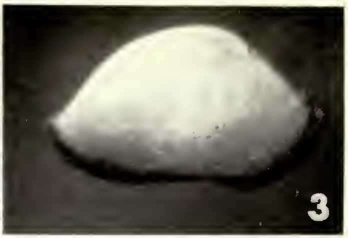
Figs 13–15. *Macrocypris tumida* Brady, lectotype, BM 80,38.17. 13. Exterior view of right valve (× 55). 14. Muscle scar pattern of left valve (× 195). 15. Exterior view of left valve (× 55), transmitted light.

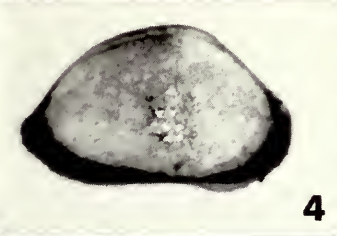
Figs 16, 17. *Aglaia clavata* Brady, lectotype, BM 81.5.1, before separation of valves (× 45), incident light. 16. Exterior view of left side. 17. Dorsal view of whole specimen.

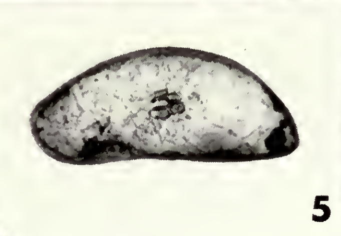
Fig. 18. *Cytherideis laevata* Brady, lectotype, BM 80.38.164 (× 45), incident light. Exterior view of right side of whole specimen before separation of valves.

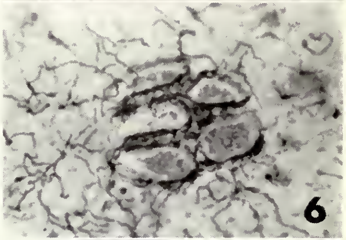

1

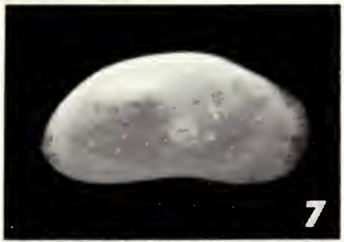

2

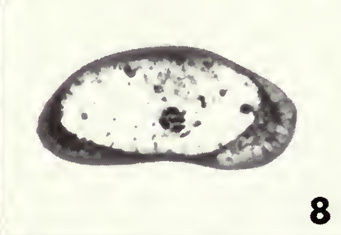

3

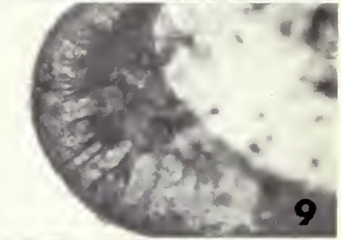

4

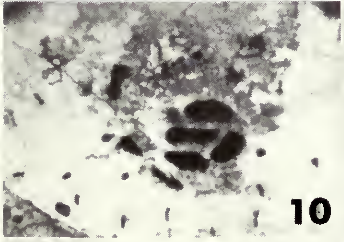

5

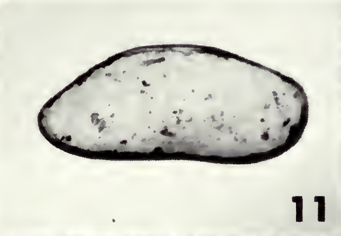

6

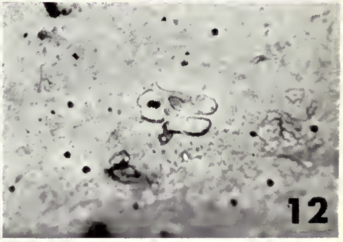

7

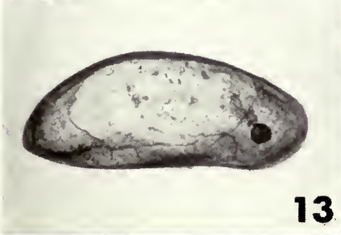

8

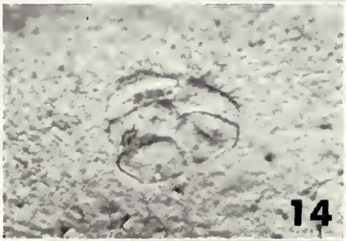

9

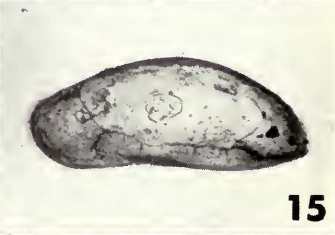

10

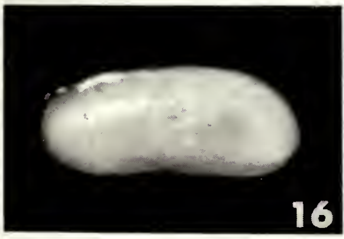

11

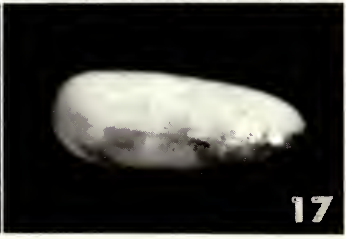

12


13


14


15


16


17

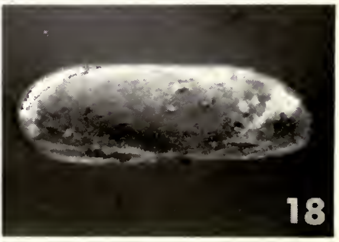

18

PLATE 3

Figs 1–5. *Cytherideis laevata* Brady, lectotype, BM 80.38.164, transmitted light. 1. External view of right valve (× 40). 2. Internal view of muscle scars of right valve (× 205). 3. External view of left valve (× 40). 4, 5. Internal views of marginal areas of right valve (× 70).

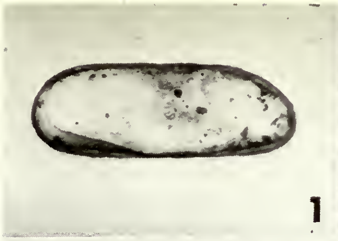
Figs 6–10. *Bythocythere* (?) *exigua* Brady, lectotype, BM 81.5.51. 6–7. External view of posteroventral margin (× 210). 8, 9. The marginal areas and hinge of whole valve (× 75). 10. The anterior hinge element (× 210).

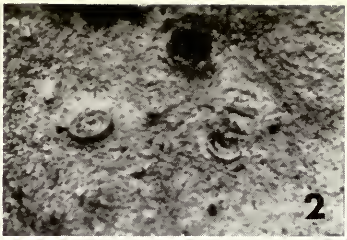
Figs 11–14. *Bairdia simplex* Brady, lectotype, BM 81.5.13 (× 25), incident light. 11–13. External and internal views of left valve. 14–15. External and internal views of right valve.

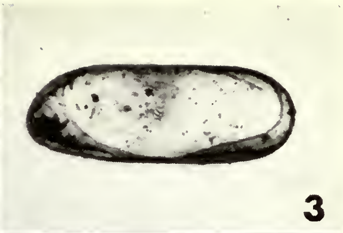
Fig. 15. *Bairdia abyssicola* Brady, lectotype, Hancock Museum (× 25), incident light. External view of right valve.

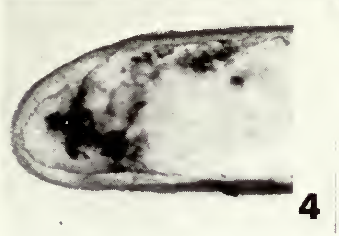
Fig. 16. *Pontocypris* (?) *subreniformis* Brady, lectotype, BM 81.5.5, Port Jackson, Australia, 2–10 fathoms (× 60), incident light, unstained. Exterior view of right valve of whole specimen.

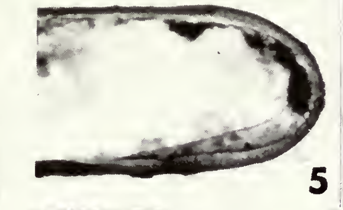
Figs 17, 18. *Bairdia minima* Brady, lectotype, BM 80.38.37 (× 50), transmitted light. Exterior views of left and right valves.

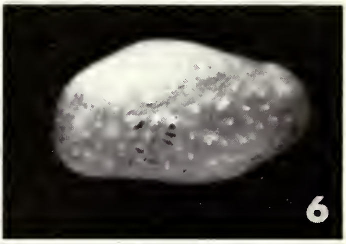

1

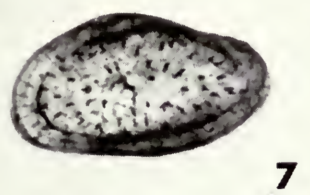

2

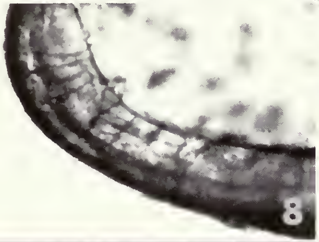

3

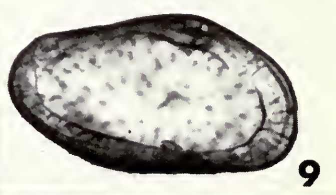

4

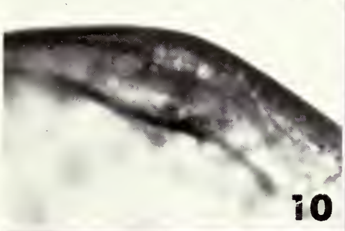

5

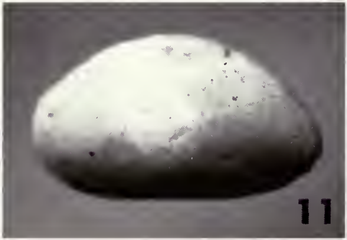

6

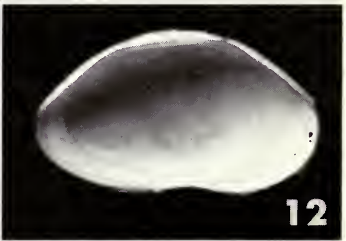

7

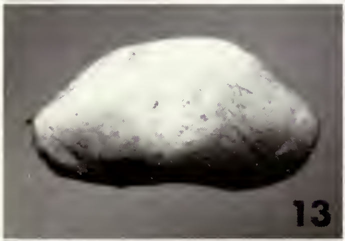

8

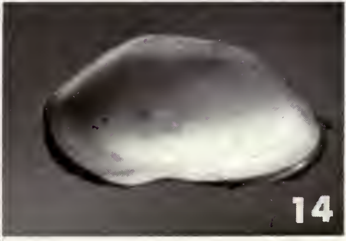

9

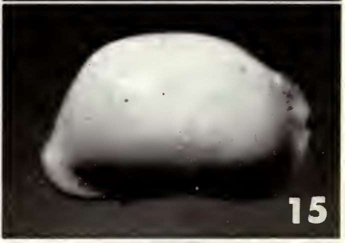

10

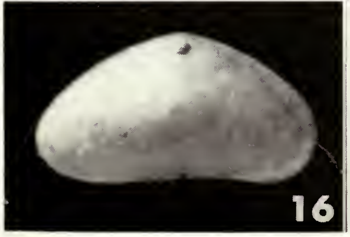

11

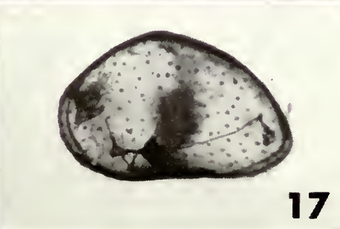

12


13


14


15


16


17

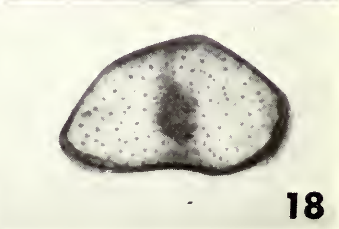

18

PLATE 4

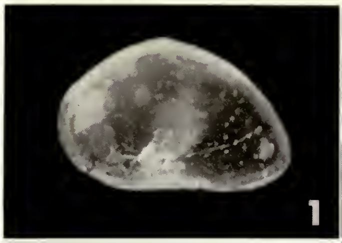
Figs 1–3. *Bairdia minima* Brady, lectotype, BM 80.38.37. 1, 3. External views of the left and right valves of what is believed to have been a whole specimen (× 50), unstained. 2. Parts of the muscle scar pattern of right valve (× 200), transmitted light, viewed from the interior.

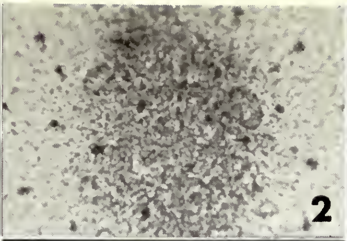
Figs 4, 5. *Bairdia hirsuta* Brady, lectotype, BM 80.38.35. 4. External view of right valve with setae still attached, transmitted light (× 25). 5. Internal view of the same valve, incident light (× 25).

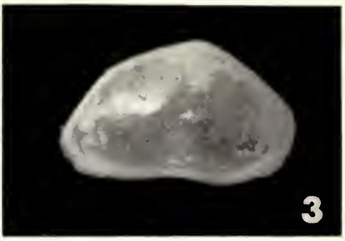
Figs 6–11. *Bairdia globulus* Brady, lectotype, BM 80.38.34. 6–7. External views of the left valves (× 35), transmitted and incident light. 8–9. External views of right valves (× 35), transmitted and incident light. 10. Internal view of muscle scar of right valve (× 90). 11. Whole specimen shown in dorsal view.

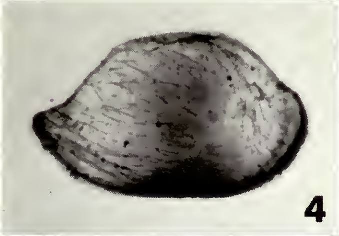
Figs 12–15. *Bairdia exaltata* Brady, lectotype, BM 81.5.10, transmitted light. 12–13. External and internal views of right valve (× 25). 14. Muscle scars of left valve (× 75). 15. External view of left valve (× 25).

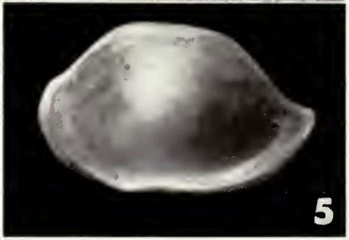
Figs 16–18. *Bairdia woodwardiana* Brady, lectotype, BM 80.38.46, transmitted light. 16. Exterior view of the right valve (× 45). 17. Muscle scars of right valve (× 95). 18. Left valve (× 45).

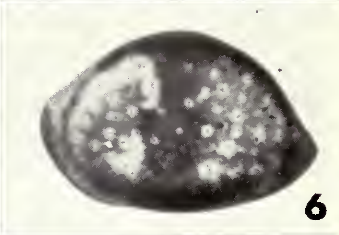

1

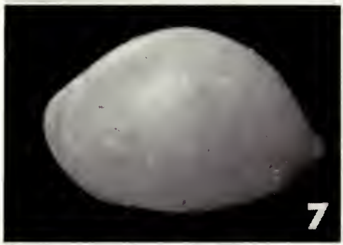

2

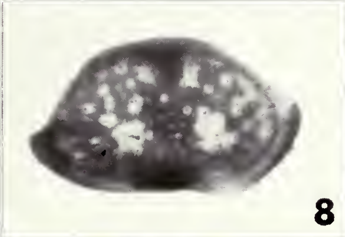

3

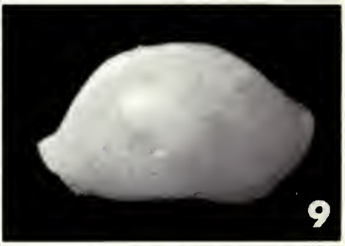

4

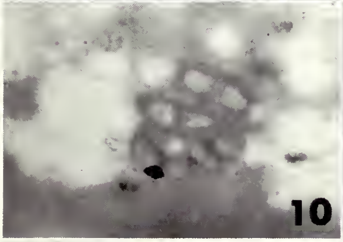

5

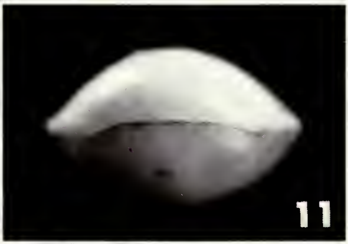

6

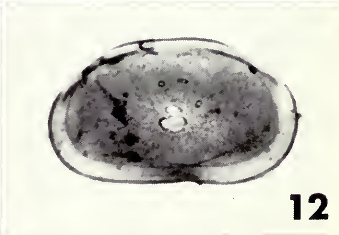

7

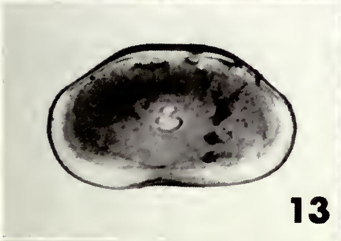

8

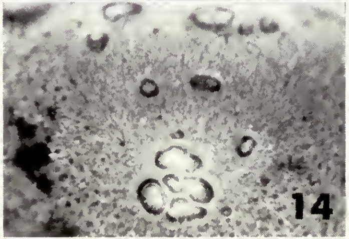

9

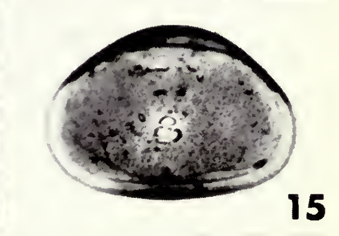

10

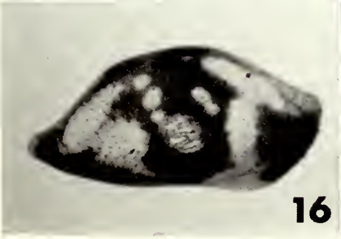

11

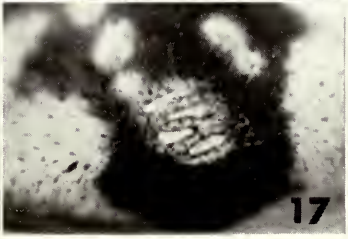

12


13


14


15


16


17

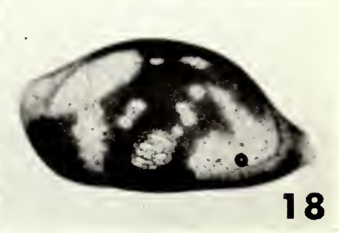

18

PLATE 5

FIGS 1–3. *Bairdia expansa* Brady, lectotype, BM 81.5.11, transmitted light. 1. External view of left valve (× 50). 2. Interior view of muscle scar of left valve (× 200). 3. External view of right valve (× 50).

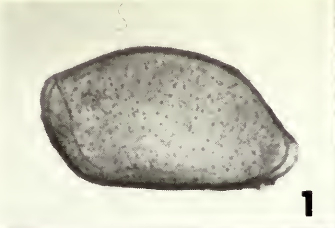
FIGS 4–6. *Bairdia attenuata* Brady, lectotype, BM 80.38.27. 4–5. Exterior and interior views of right valve of a complete specimen (× 30), incident light. 6. Muscle scar of interior of same valve (× 85).

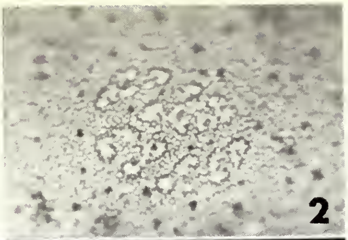
FIGS 7–9. *Bairdia fortificata* Brady, lectotype, BM 81.5.12. 7. External view of left valve (× 35). 8. Internal view of left valve (× 35). 9. External view of muscle scar region showing some of the scars and the finely punctate surface (× 100).

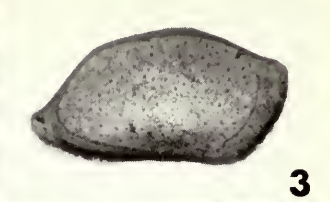
FIGS 10–12. *Cythere obtusalata* Brady, lectotype, BM 80.38.96. 10, 11. Exterior and interior view of right valve (× 60), incident light, stained. 12. Interior view of valve showing muscle scar and surface reticulation (× 185), transmitted light.

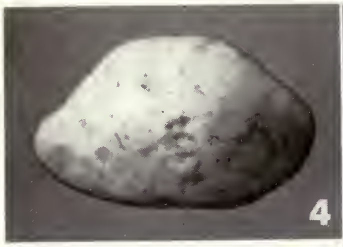
FIGS 13–15. *Cythere vellicata* Brady, lectotype, BM 81.5.32, incident light, stained. 13. Exterior view of the right valve. 14, 15. Dorsal aspects of whole specimen (× 170).

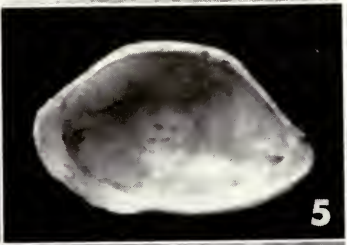
FIGS 16–19. *Cythere curvicostata* Brady, lectotype, BM 80.38.64 (× 50), incident light, stained. 16. Exterior dorsal view. 17. Exterior of left valve. 18. Ventral aspect. 19. Right valve of a complete specimen.

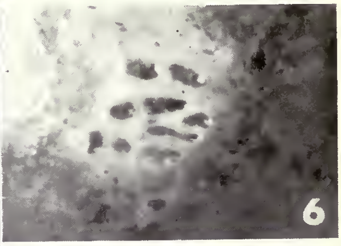

1

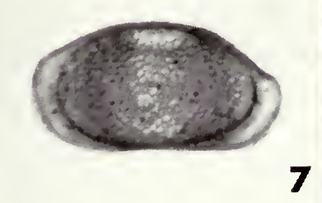

2

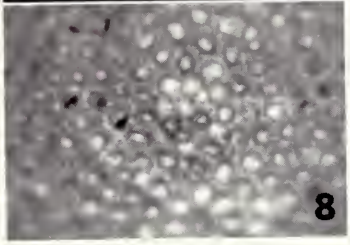

3

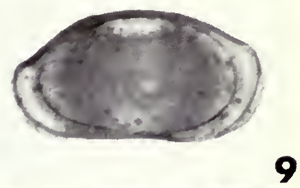

4

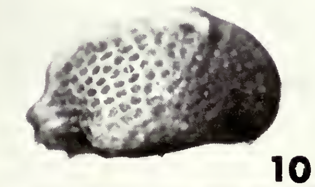

5

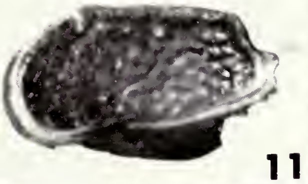

6

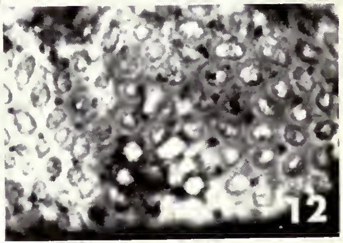

7

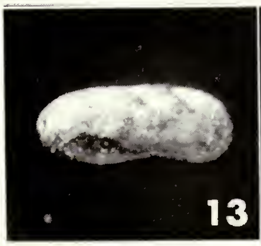

8

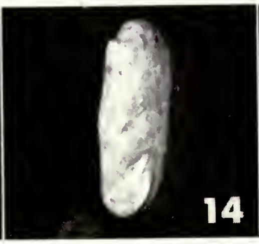

9

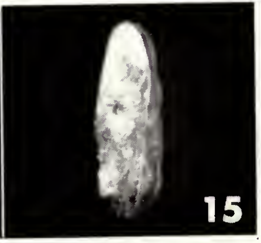

10

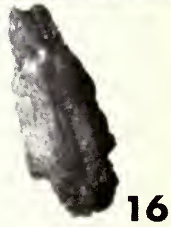

11

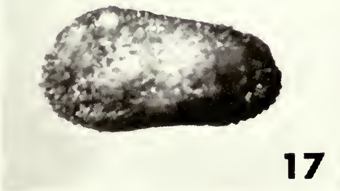

12


13


14


15


16


17

18

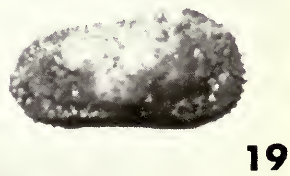

19

PLATE 6

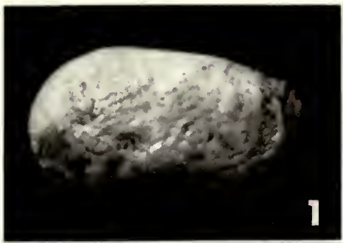
FIGS 1–3. *Cythere moseleyi* Brady, lectotype, BM 80.38.93, male (× 50), incident light, stained. 1. External view of left side. 2. Dorsal view. 3. External right side.

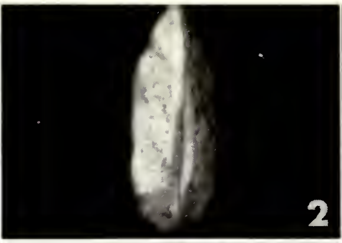
FIG. 4. *Cythere falklandi* Brady, BM 80.38.78A (× 50), incident light, unstained. External view of left valve.

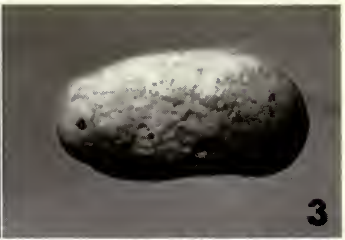
FIGS 5–9. *Cythere falklandi* Brady, BM 80.38.78B. 5–6. Transmitted light views of right valve (× 50). 7. Internal view of the muscle scars (× 155). 8. Anterior marginal area (× 170) showing radial pore canals and vestibule. 9. External view of same specimen (× 50), transmitted light, unstained.

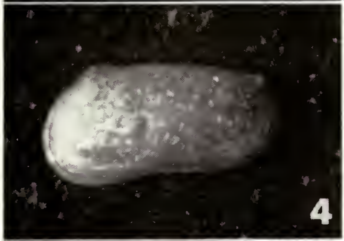
FIGS 10–12. *Cythere inconspicua* Brady, lectotype, BM 81.5.22, whole specimen, inverted to illuminate ventrolateral ridges within the subtle reticulate pattern (× 80), stained. 10. External view of left side. 11. Dorsal view. 12. Ventrolateral quarter.

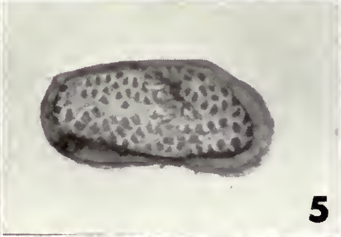
FIGS 13–18. *Cythere cumulus* Brady, lectotype, BM 81.5.17. 13, 14. External views of right and left valves. 15. Dorsum of whole specimen (× 50), incident light, stained. 16, 18. Internal views of posterior and anterior elements of hinge and radial pore canals. 17. Muscle scars and reticulate surface pattern (× 165), transmitted light.

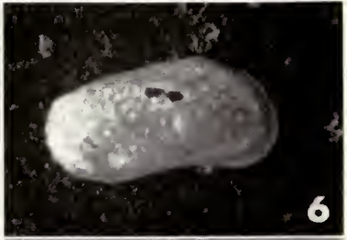

1

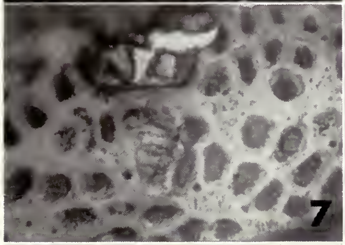

2

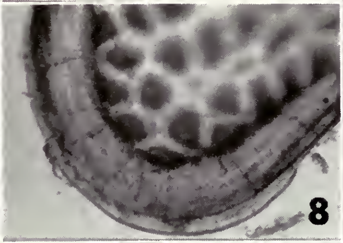

3

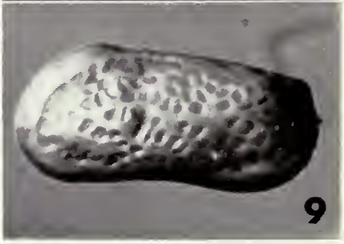

4

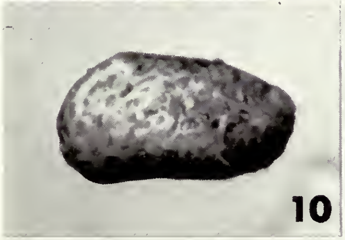

5

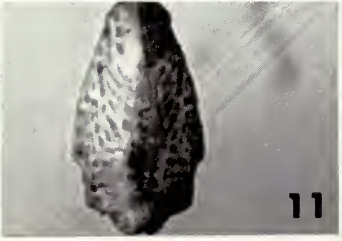

6

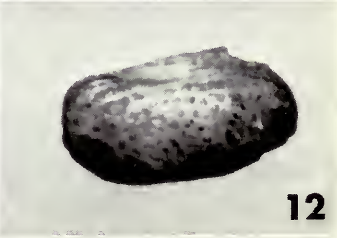

7

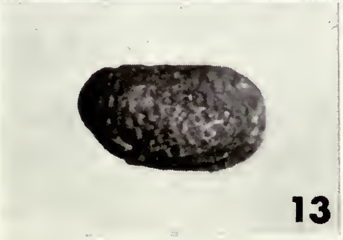

8

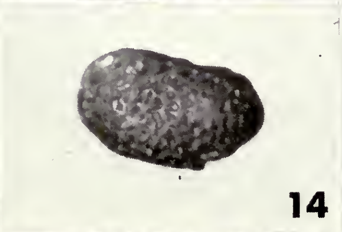

9

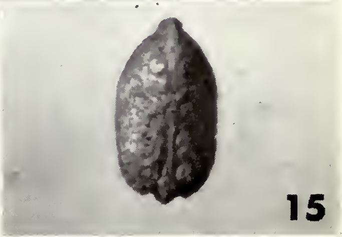

10

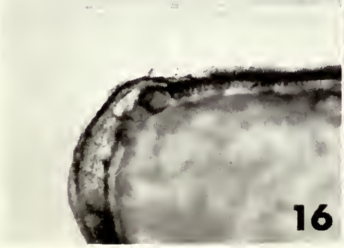

11

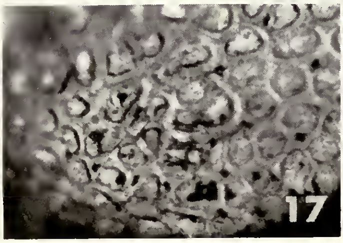

12


13


14


15


16


17

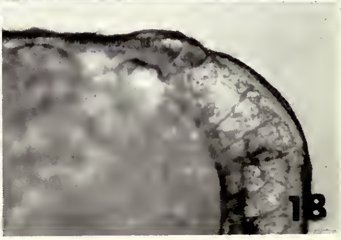

18

PLATE 7

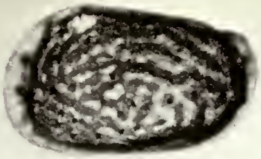
Figs 1–4, 6, 7. *Cythere floscardui* Brady, lectotype, BM 80.38.80. 1, 3. External views of left and right valves (× 80), transmitted light. 2. Muscle scars with V-shaped antennal scar, and reticulate surface pattern (× 65). 4, 6, 7. Views of left, dorsal, and right sides of whole specimen before separation (× 45), incident light, stained.

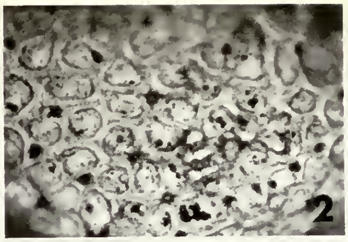
Fig. 5. *Cythere cumulus* Brady, lectotype, BM 81.5.17. Dorsal view (× 40).

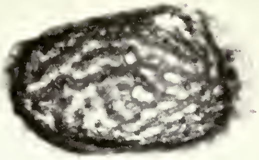
Figs 8, 11. *Cythere securifer* Brady, lectotype, BM 80.38.112 (× 60). 8, 11. External and internal views of left valve of a female.

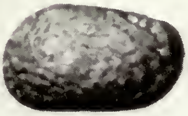
Figs 9, 10, 12–15. BM 80.38.112A. 9, 10. External views of left and right sides of whole specimen (× 55), showing apparently dimorphic posteroventral velate structure ('triangular or hatchet-shaped protuberance'), transmitted light views of selected portions of the valves including, 12. Muscle scars and surface reticulation (× 135). 13. Anterior marginal area (note antennule and part of antenna). 14, 15. Anterior and posterior hinge elements (× 110).

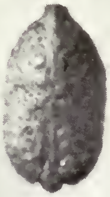
Figs 16–19. *Cythere exfoveolata* Neviani, lectotype, BM 80.38.81 (× 55), whole carapace of male. 16. External view of lateroventral quarter. 17. Right side. 18. Dorsum. 19. Left side.

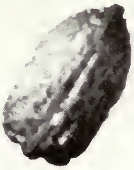

1

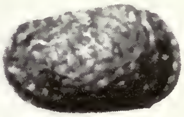

2

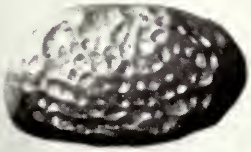

3

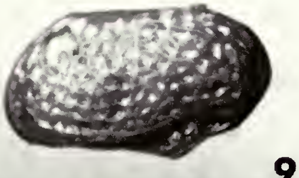

4

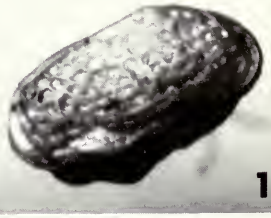

5

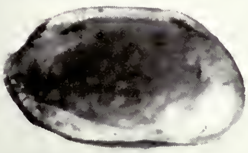

6

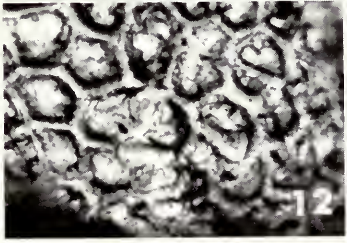

7

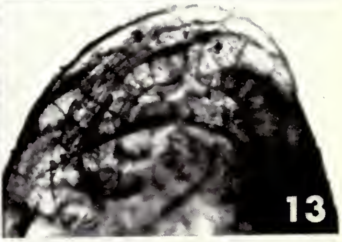

8

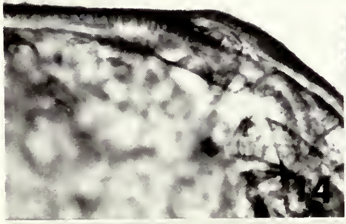

9

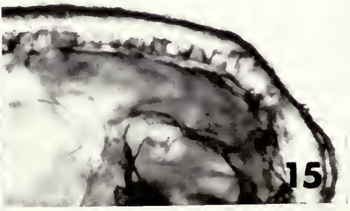

10

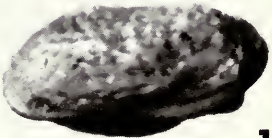

11

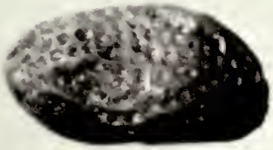

12

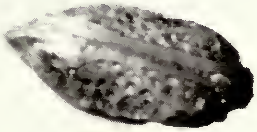

13


14


15


16


17


18

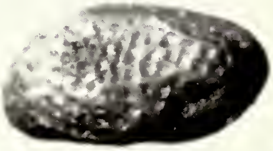

19

PLATE 8

Figs 1–4. *Cythere flabellicostata* Brady, lectotype, BM 80.38.79 (× 50). 1. External views of whole specimen from right, incident light. 2. Right side, black light. 3. Left side, incident light. 4. Left side, black light.

Fig. 5. *Cythere acupunctata* Brady, lectotype, BM 80.38.50. External view of left valve of a complete specimen (× 35), incident light, stained.

Figs 6, 7. *Cythere scintillulata* Brady, lectotype, BM 80.38.110. 6. External view of left valve of an articulated specimen (× 55), incident light, unstained. 7. External view of left valve (× 65), incident light, unstained.

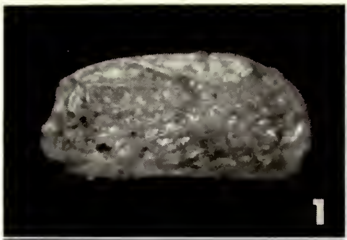
Figs 8, 9. *Cythere hardingi* Puri & Hulings, lectotype, BM 80.38.97. 8. External view of whole specimen as seen from left side (× 45). 9. The top (× 40).

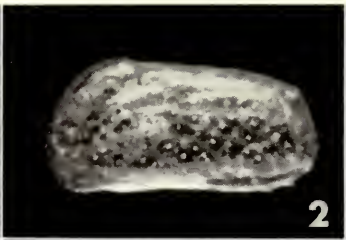
Figs 10–12. *Cythere fulvotincta* Brady, lectotype, BM 81.5.21 (× 55), incident light, stained. 10. External view of whole specimen as seen from left side. 11. The top. 12. Right side.

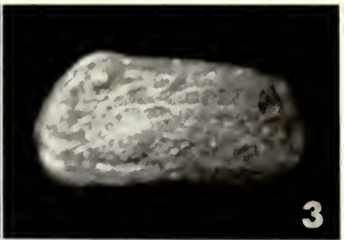
Figs 13, 14. *Cythere lubbockiana* Brady, lectotype, BM 81.5.25. 13. External view of whole specimen as seen from left high oblique side (× 40). 14. Right high oblique side (× 45), incident light, stained.

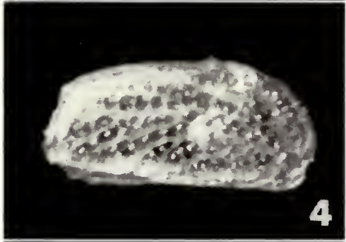
Figs 15–18. *Cythere parallelogramma* Brady, lectotype, BM 80.38.99. 15. External view of right valve. 16. Internal view of right valve (both × 40, incident light, stained). 17. Muscle scars as seen in transmitted light in interior of right valve (× 130). 18. Top view showing stepped anterior tooth and prominent posterior tooth of holamphidont hinge (× 40).

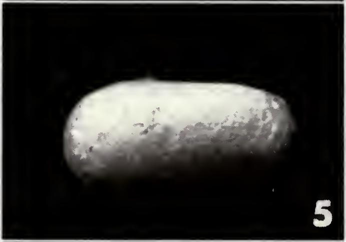
PLATE 8

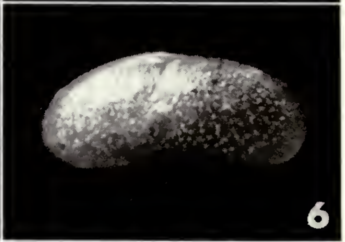

1

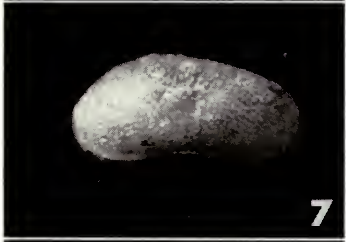

2

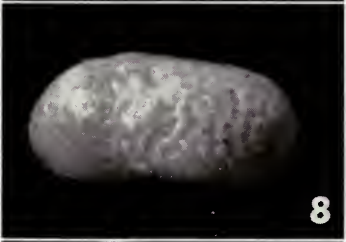

3

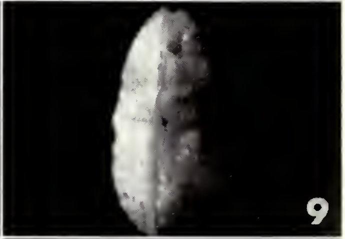

4

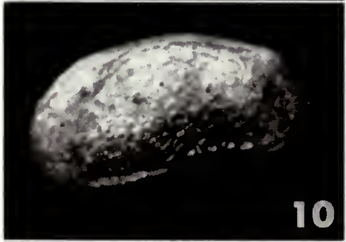

5

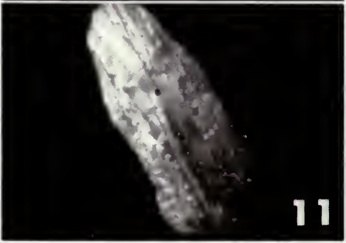

6

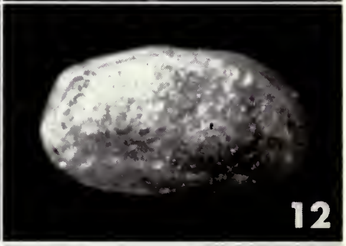

7

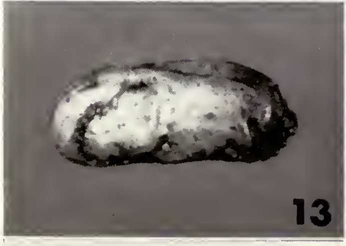

8

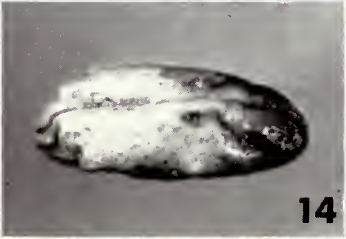

9

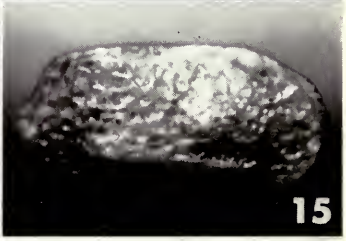

10

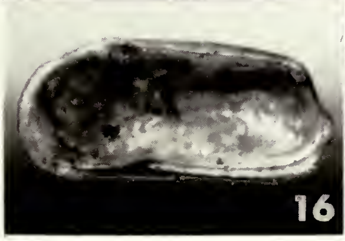

11

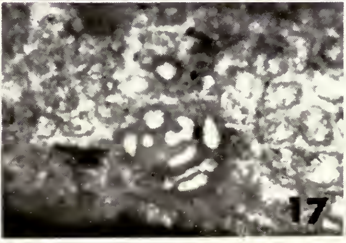

12


13


14


15


16


17

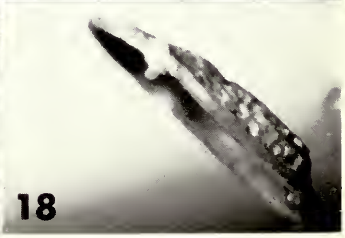

18

PLATE 9

Figs 1–4. *Cythere mackenziei* Puri & Hulings, lectotype, BM 80.38.103. 1. Interior view of left valve (× 35), transmitted light, unstained. 2. Muscle scar (× 170). 3. Hinge (× 70). 4. Radial pore canals of anterior margin (× 155).

Figs 5, 6. *Cythere cytheropteroides* Brady, lectotype, BM 80.38.67 (× 40), incident light, stained. 5. External view of right valve. 6. Internal view of right valve.

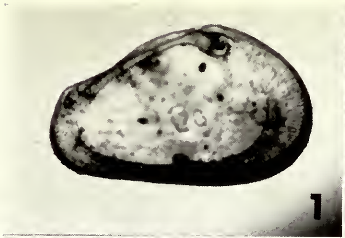
Figs 7, 8. Lectotype, BM 80.38.67. 7. External view of right valve (× 35), incident light, stained. 8. Internal view of anterior hinge element (× 105).

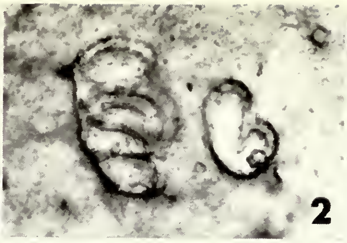
Fig. 9. *Cythere rastromarginata* Brady, paralectotype, BM 80.38.104 (× 60), incident light, unstained. External lateral right valve view of probable female.

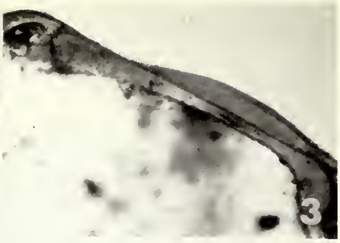
Figs 10–14. Lectotype, BM 80.38.105. 10–12. External lateral and internal views of left valve of male (× 60), incident and transmitted light, stained. 13. Posteroventral marginal area. 14. Right side of the subcentral tubercle (× 185).

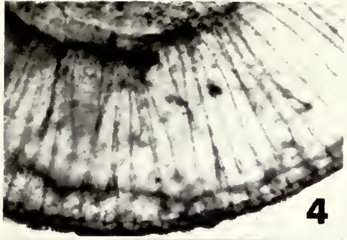
Figs 15, 16. *Cythere impluta* Brady, lectotype, BM 1961.12.4.30 (× 45), incident light, stained. 15. External left lateral view of whole specimen. 16. Dorsal view of whole specimen.

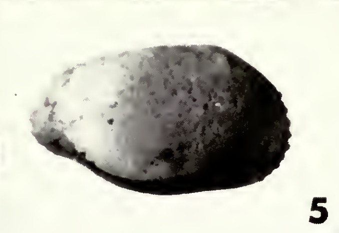
Figs 17–19. *Cythere murrayana* Brady, lectotype, BM 80.38.94 (× 75), incident light, unstained. 17. External view of left valve. 18. Dorsum of whole specimen. 19. Venter of whole specimen.

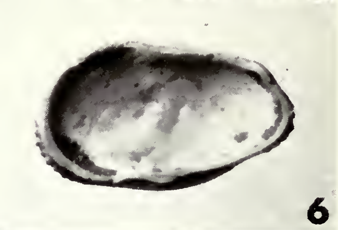

1

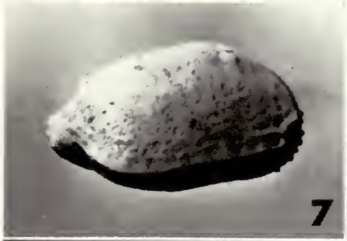

2

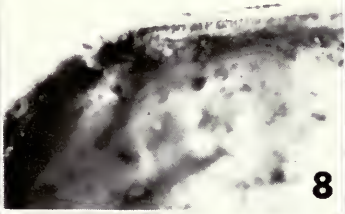

3

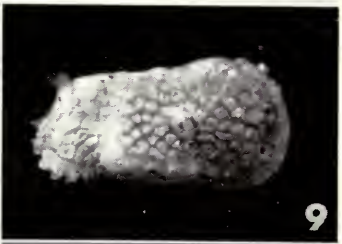

4

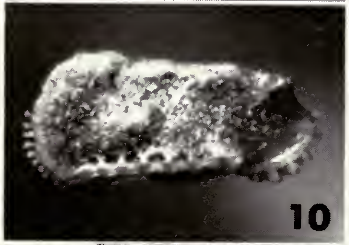

5

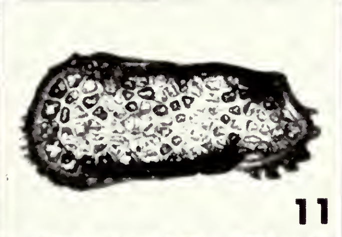

6

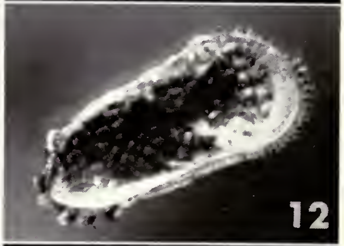

7

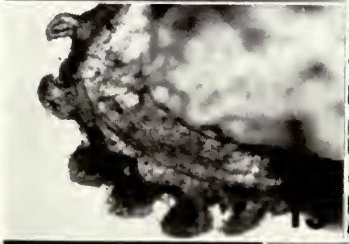

8

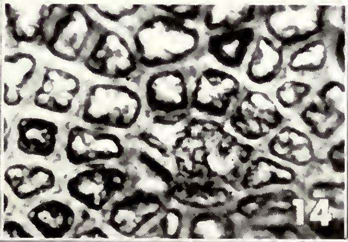

9

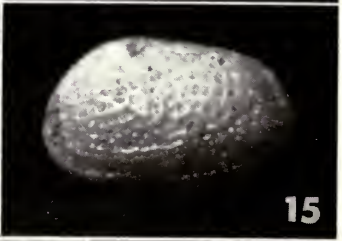

10

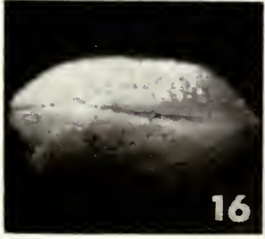

11

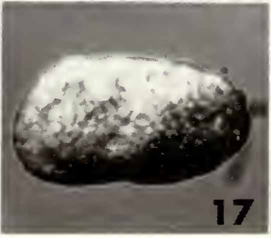

12

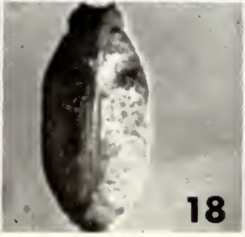

13


14


15


16


17


18

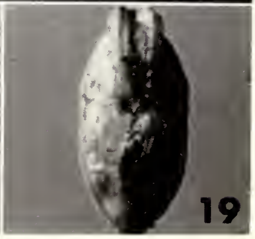
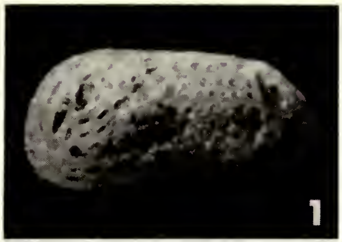

19

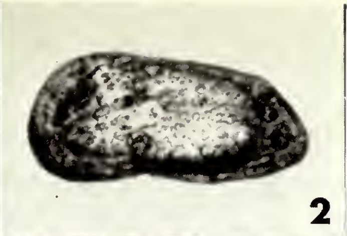
PLATE 10

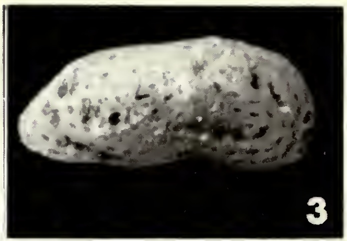
FIGS 1–11. *Cythere exilis* Brady, lectotype, BM 81.5.20, figs 5, 6 (× 145), transmitted light. 1–2. External lateral views of left valves. 3–4. External lateral views of right valves (all × 45, incident and transmitted light, stained). 5. Area postjacent to subcentral tubercle of left valve showing configuration of fossae. 6. Interior view of anterior margin of right valve. 7. Posterior margin of right valve. 8. Anterior hinge element of left valve. 9. Anterior hinge element of right valve. 10. Posterior hinge element of right valve. 11. Posterior hinge element of left valve.

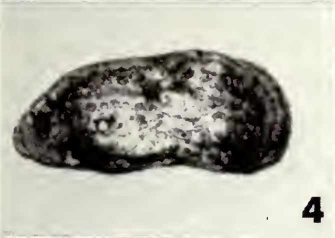
FIGS 12, 13. *Cythere bicarinata* Brady, lectotype, BM 80.38.50 (× 50), incident light, stained. 12. External view of right valve. 13. Dorsum of whole carapace.

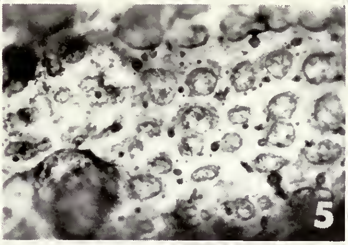
FIGS 14–18. *Cythere ericea* Brady, lectotype, BM 80.38.76, figs 16–18 (× 90), incident and transmitted light, stained. 14. External view of right valve (× 30), incident light, stained. 15. Internal view of right valve. 16. Internal anterior hinge element. 17. Muscle scars. 18. Posterior hinge element of right valve.

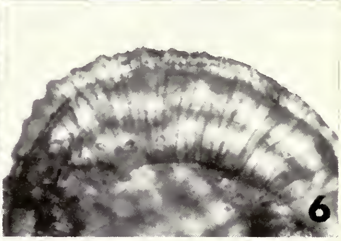

1

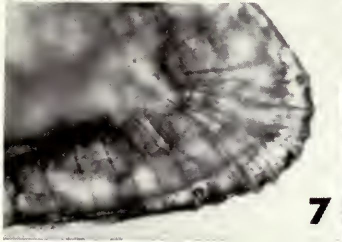

2

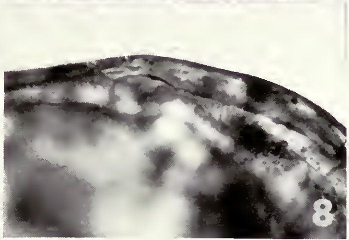

3

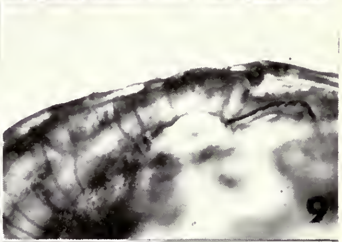

4

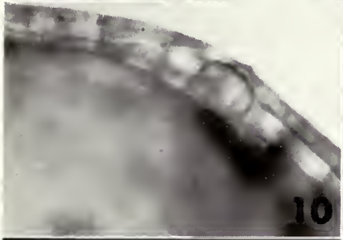

5

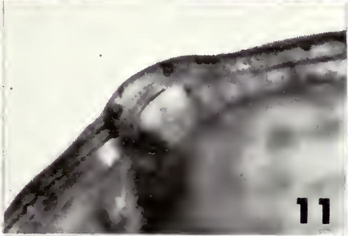

6

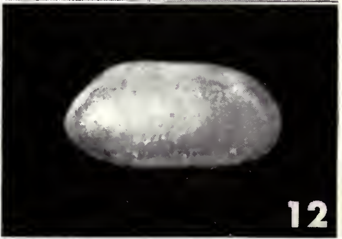

7

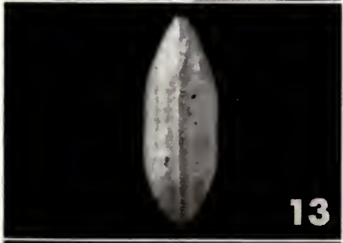

8

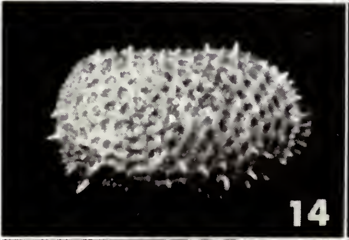

9

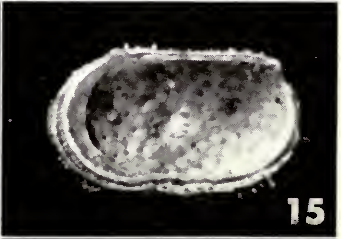

10

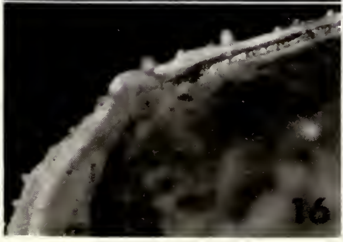

11

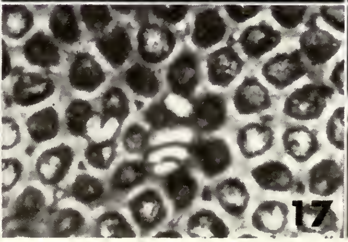

12


13


14


15


16


17

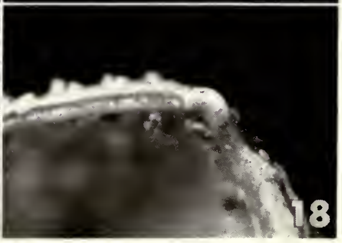

18

PLATE 11

Figs 1–9. *Cythere irpex* Brady, lectotype, BM 80.38.86. 1–3. External lateral views of left and right valves. 4. Internal view of right valve (all × 70), black light and transmitted light, unstained. 5. Enlarged internal view of muscle scars. 6. Anterior hinge element of right valve. 7–8. Posterior hinge element of left and right valves. 9. Anterior hinge element of left valve (all × 200), transmitted light.

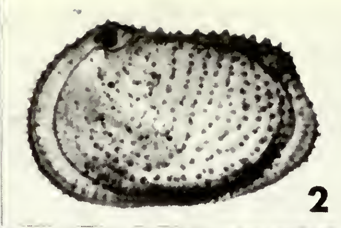
Figs 10, 11. *Cythere dasyderma* Brady, lectotype, BM 1961.12.4.39, showing subreticulate, spinose surface, imperfectly developed holamphidont (penultimate stage ?) hinge and large V-shaped frontal muscle scar (× 25), incident light, stained. 10. External lateral view of right valve. 11. Internal lateral view of left valve.

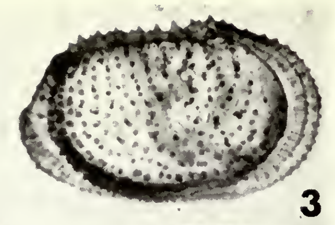
Figs 12–14. *Cythere irrorata* Brady, lectotype, BM 80.38.86A (× 45), incident light, unstained. 12. External view of left valve. 13. Venter of whole specimen. 14. Dorsum of whole specimen.

Fig. 15. *Cythere viminea* Brady, lectotype, BM 81.5.33 (× 50), incident light, unstained, photograph taken of specimen on original museum slide. External view of broken right valve.

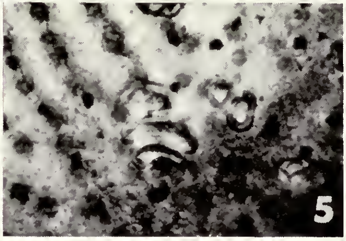
Figs 16–18. *Cythere acanthoderma* Brady, lectotype, BM 80.38.48A. 16. External view of late instar left valve. 17. Internal view of late instar left valve (both × 35, incident and transmitted light, unstained). 18. Enlargement of anterior hinge element and marginal area (× 90).

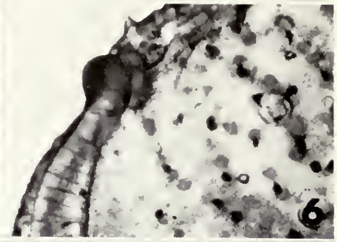
1

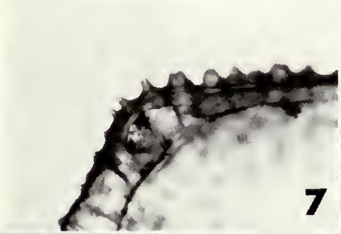

2

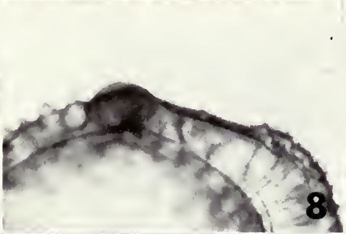

3

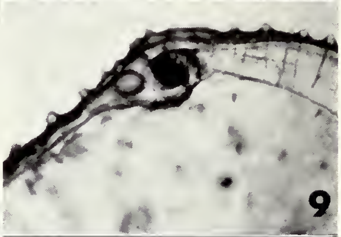
4

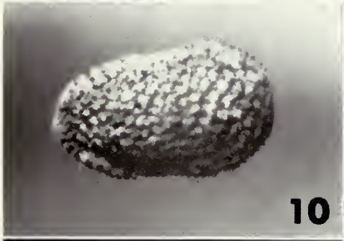

5


6

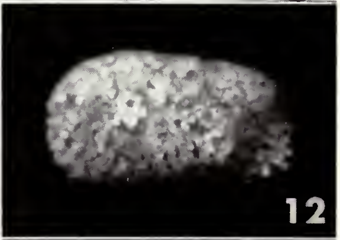

7


8

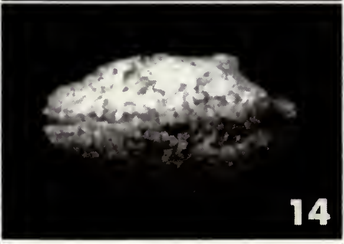

9

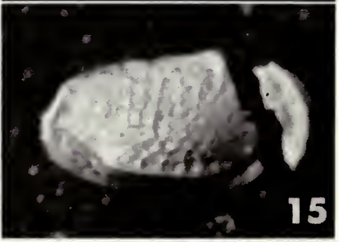

10

11


12

13


14


15

16

17

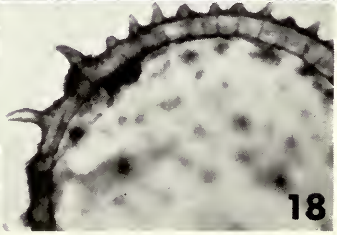

18

PLATE 12

FIGS 1–3. *Cythere sabulosa* Brady, lectotype, BM 80.38.107. 1, 2. External views of right and left valves. 3. Dorsum of whole specimen (×55 and ×40), incident light, stained.

FIGS 4–6. *Cythere packardi* Brady, lectotype, BM 81.5.26 (×65), incident light, stained. 4. External view of left valve. 5, 6. Dorsum and right valve of whole specimen.

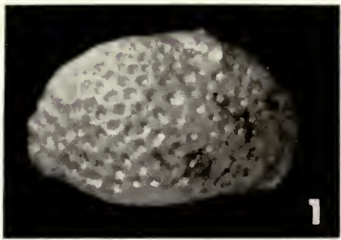
FIGS 7–9. *Cythere radula* Brady, lectotype, BM 81.5.28 (×35), incident light, stained. 7. External lateral view of left valve, late instar. 8. Internal view of left valve of late instar. 9. Dorsal view.

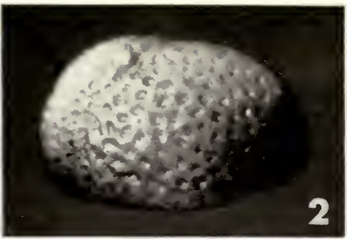
FIGS 10,11. *Cythere lepralioides* Brady, lectotype, BM 80.38.91 (×45), incident light, stained. External and internal views of right valve of probable late instar.

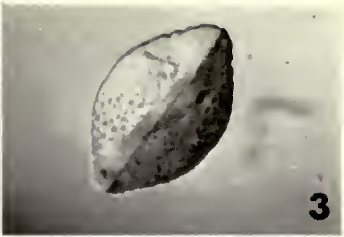
FIGS 12, 13. *Cythere torresi* Brady, lectotype, BM 81.5.31 (×90), transmitted light, unstained. 12. Internal lateral view of right valve. 13. External lateral view of right valve.

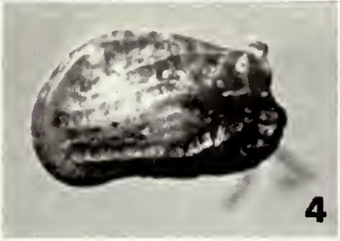
FIGS 14–16. *Cythere kerguelenensis* Brady, lectotype, BM 80.38.88 (×50), incident light, stained. 14. External view left of whole specimen. 15. Right side. 16. Dorsum.

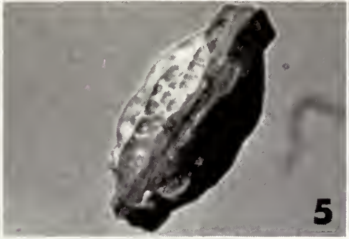
FIGS 17, 18. Lectotype, BM 80.38.88 (×50), incident light, stained. 17. External view of separated left valve. 18. External view of separated right valve.

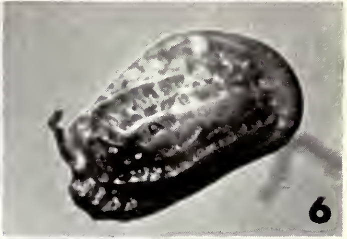

1

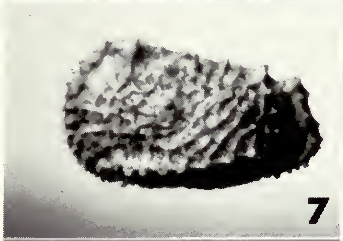

2

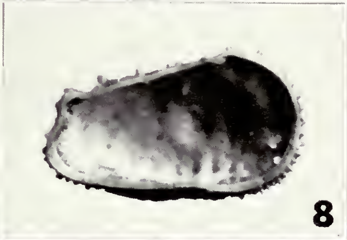

3

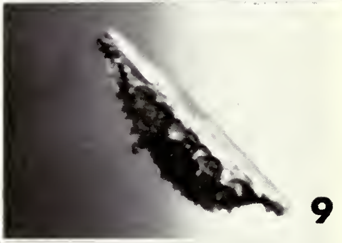

4

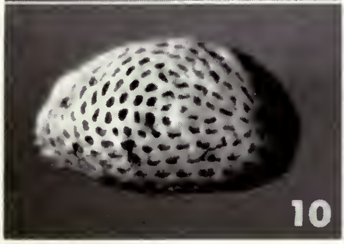

5

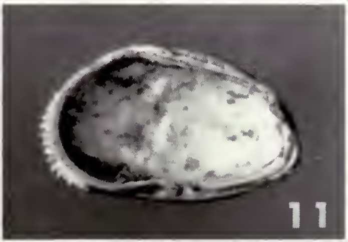

6

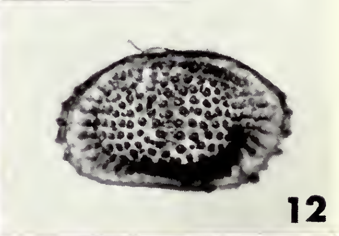

7

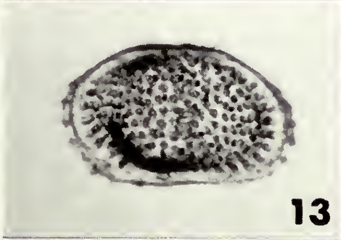

8

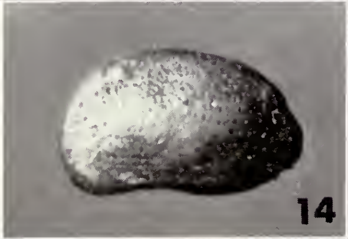

9

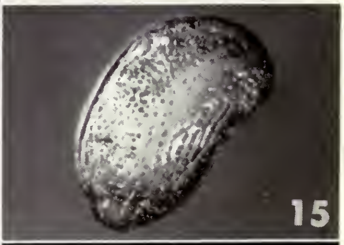

10

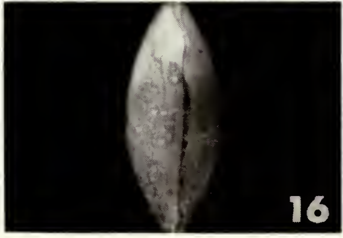

11

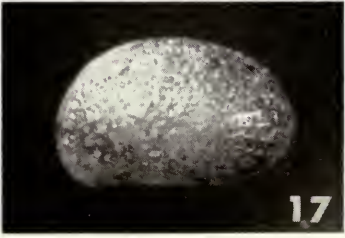

12


13


14


15


16


17

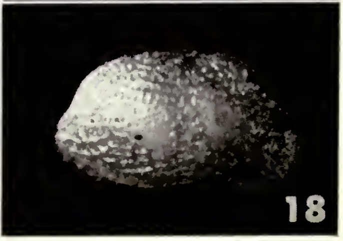
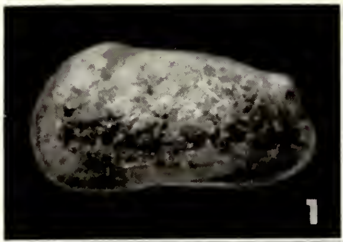
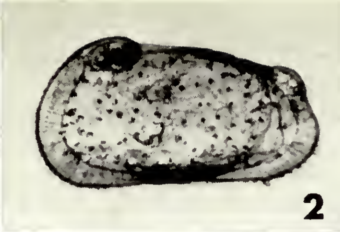

18

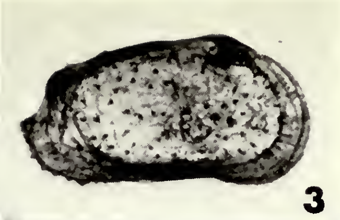
PLATE 13

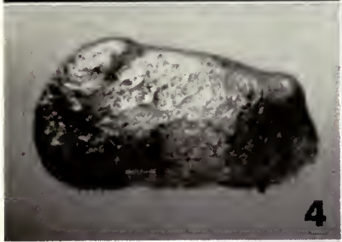
Figs 1–9. *Cythere subrufa* Brady, lectotype, BM 80.38.117. 1–5. External lateral views of left and right valves (×80), incident and transmitted light, unstained and stained. 6. Internal view of right valve (×80). 7–8. Internal views of anterior and posterior hinge elements of left valve. 9. Muscle scar pattern of right valve (×305), incident and transmitted light.

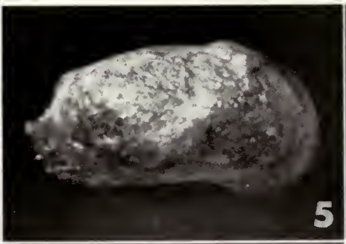
Figs 10–18. *Cythere wyvillethomsoni* (Brady), lectotype, BM 80.38.123. 10,11. External views of left and right valves (×40), incident light, stained. 12–17. (×140.) 12. Interior view of enlarged anteroventral portion of left valve showing radial pore canals. 13. Anterior hinge element of left valve. 14. Posterior hinge element of right valve. 15. Posteroventral marginal area of left valve. 16. Anterior hinge element of right valve. 17. Posterior hinge element of left valve. 18. Second antenna and penis dissected from original complete specimen (×86).

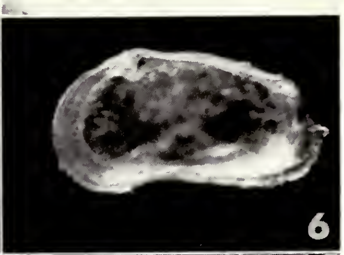

1

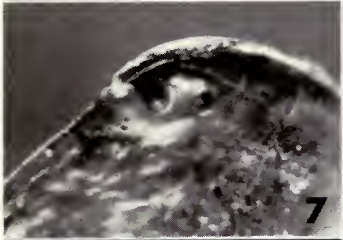

2

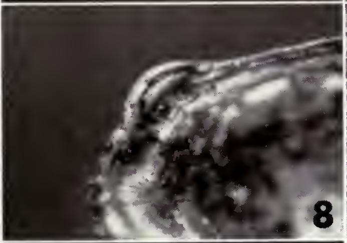

3

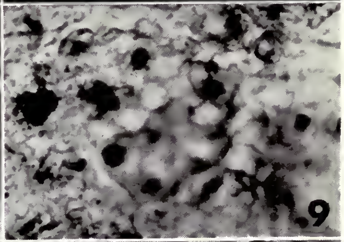

4

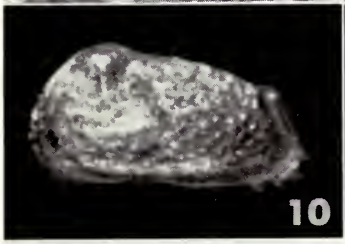

5

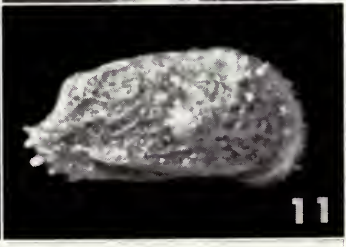

6

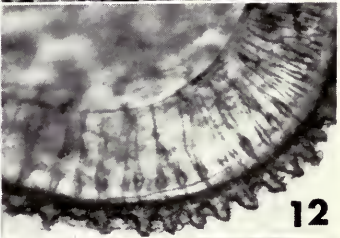

7

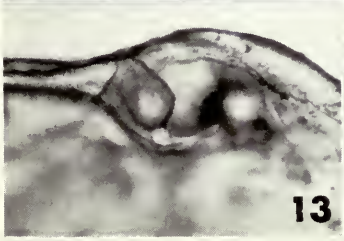

8

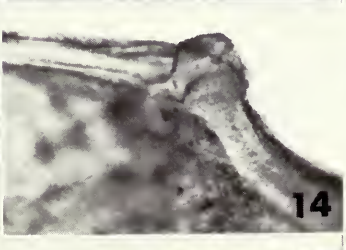

9

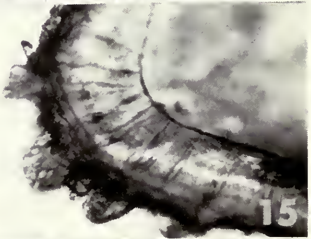

10

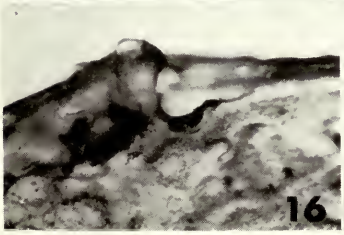

11

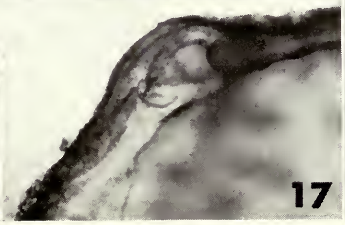

12


13


14


15


16


17

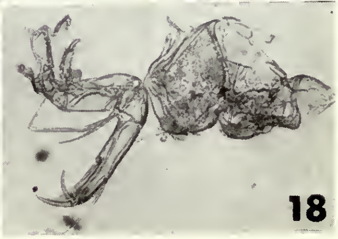

18

PLATE 14

FIGS 1–3. *Cythere wyvillethomsoni* Brady, lectotype, BM 80.38.123. 1. External lateral view of right valve (×45), transmitted light. 2. Region postjacent to subcentral tubercle showing reticulate surface pattern in relation to normal pore canals (×155). 3. Lateral view of left valve (×45).

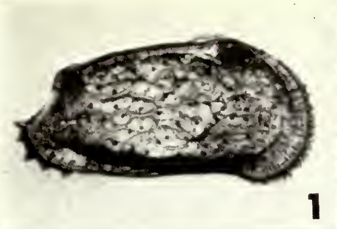
FIG. 4. *Cythere stolonifera* Brady, lectotype, BM 80.38.115 (×50), incident light, unstained. External lateral left valve view of broken complete specimen.

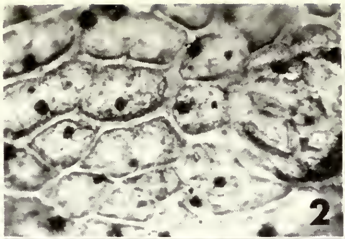
FIGS 5–8. *Cythere lauta* Brady, lectotype, BM 81.5.24. 5–6. External views of right valve (×65), incident light in air and immersed in water, stained. 7. Dorsal view. 8. Left valve (both ×65), incident light, immersed in water.

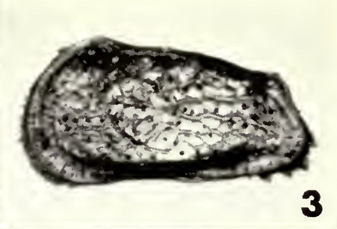
FIGS 9–12. *Cythere craticula* Brady, lectotype, BM 81.5.16. 9–10. External lateral views of left valve (×45), incident and transmitted light, unstained. 11. Internal view showing hinge and portions of marginal area (×70). 12. Area postjacent and ventral to subcentral tubercule (×120).

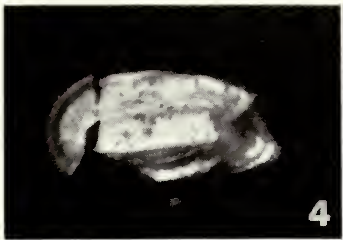
FIG. 13. *Cythere scalaris* Brady, lectotype, BM 80.38.109 (×35), incident light, photograph taken of specimen on original museum slide. External view of broken right valve.

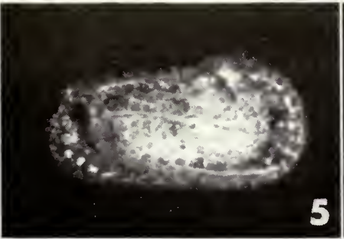
FIGS 14–18. *Cythere quadriaculeata* Brady, lectotype, BM 80.38.50. 14. External lateral view of whole specimen. 15. Dorsal view of whole specimen (both ×50), incident light, stained. 16, 17. Internal views of hinges of right and left valves. 18. Anterior marginal area showing radial pore canals (16–18, ×105), transmitted light.

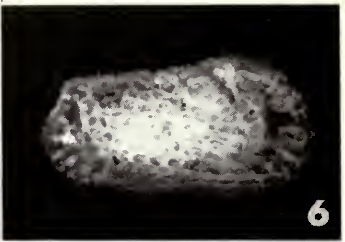

1

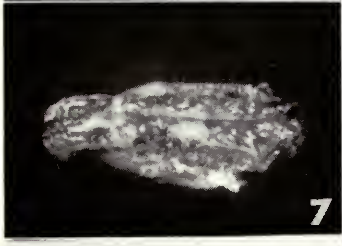

2

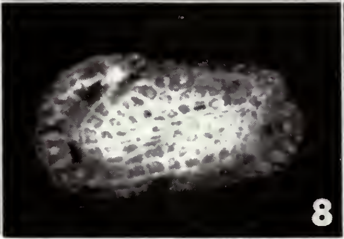

3

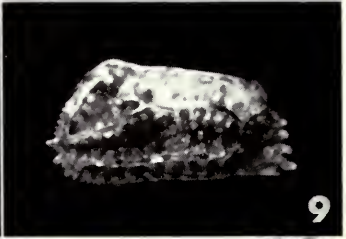

4

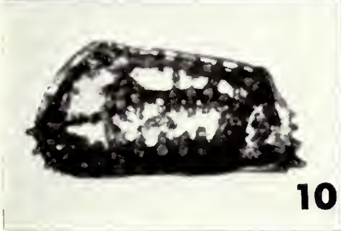

5

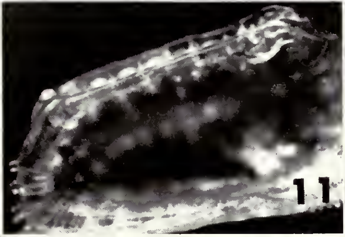

6

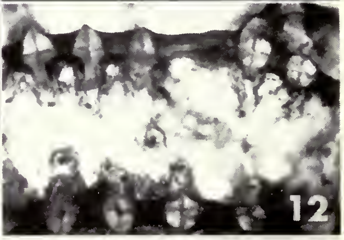

7

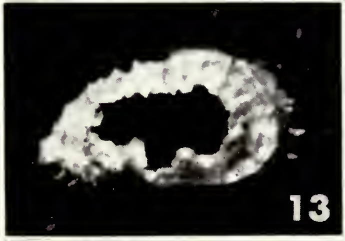

8

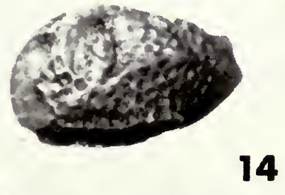

9

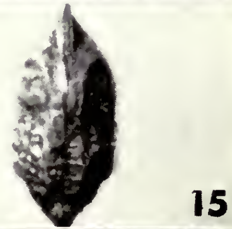

10

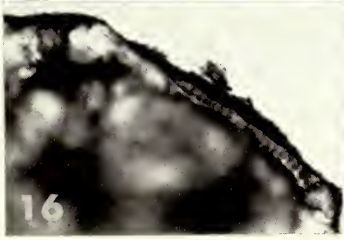

11

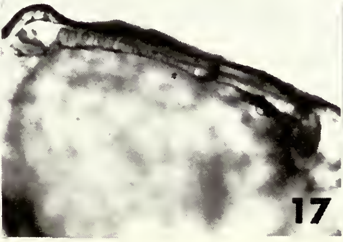

12


13


14


15


16


17

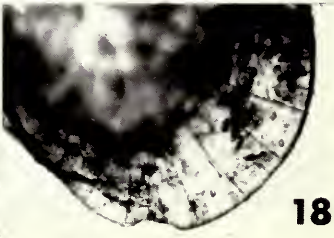

18

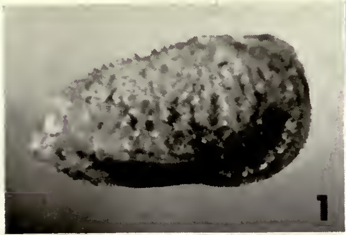
PLATE 15

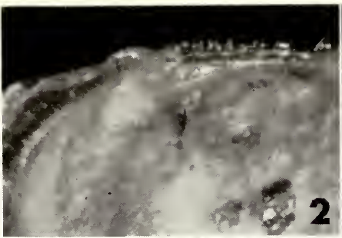
Figs 1–4. *Cythere dorsoserrata* Brady, lectotype, BM 81.5.19. 1. External lateral view of right valve (× 45), incident light, stained. 2. Internal view of anterior hinge element. 3. Internal view of posterior hinge element. 4. Anterior portion of marginal area (2–4, × 105), incident light, stained.

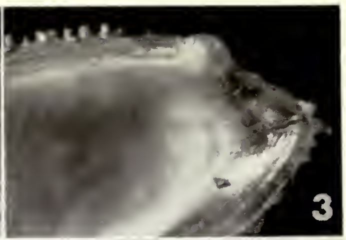
Figs 5–8. *Cythere patagoniensis* Brady, lectotype, BM 81.5.27. 5. External view of left valve. 6. External view of right valve. 7. Dorsum view of whole specimen. 8. Venter view of whole specimen.

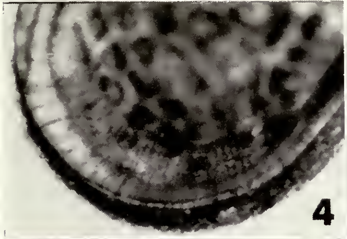
Figs 9–16. *Cythere velivola* Brady, lectotype, BM 80.38.122. 9. External lateral view of left valve (× 45), black light, immersed in water. 10. Interior view of left valve (× 45), transmitted light. 11. Interior view of muscle scar region showing normal pore canals. 12. Anterior marginal area showing radial pore canals (both × 160), transmitted light; the sieve-like nature of the normal pore canals may be an optical artifact caused by air trapped in the canals in contact with the parallel oriented C-axes of the calcite crystals of the carapace wall. 13, 14. Dorsal views of posterior and anterior teeth of hinge of right valve. 15, 16. Plate-shaped spines of ventrolateral velate flange, and plates of dorsal crest (13–16, about × 205), transmitted light.

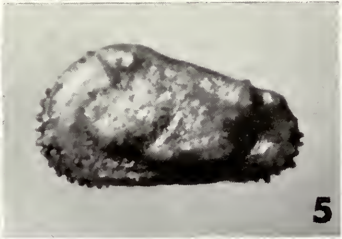
Figs 17, 18. *Cythere tricristata* Brady, lectotype, BM 80.38.121 (× 50), incident light, stained. 17. External view of right valve. 18. Dorsum of whole carapace.

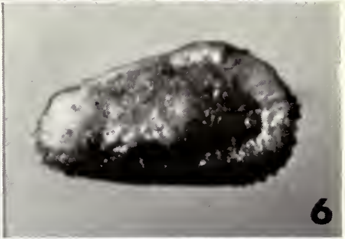

1

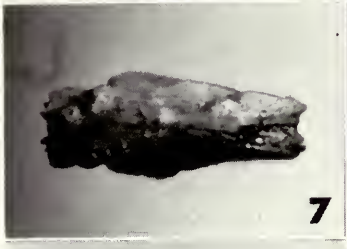

2

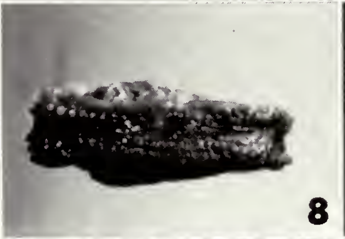

3

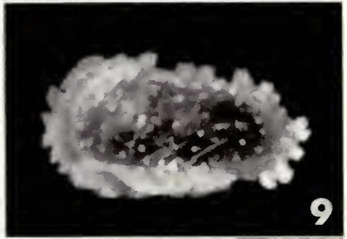

4

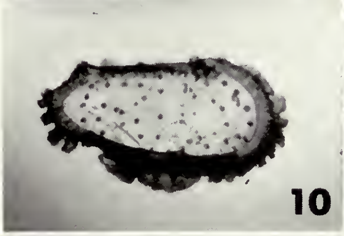

5

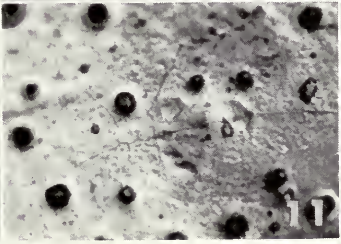

6

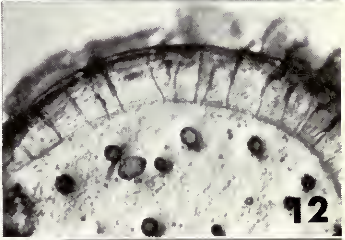

7

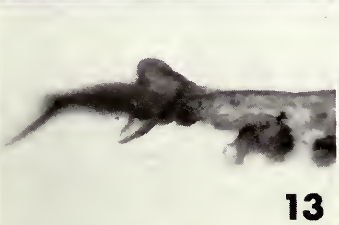

8

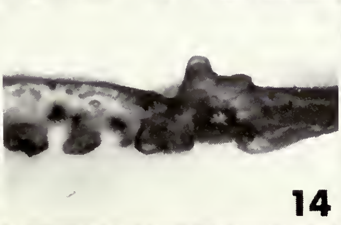

9

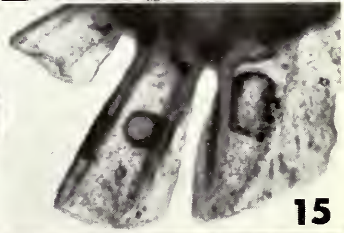

10

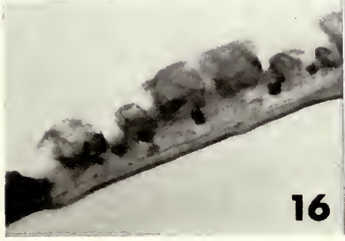

11

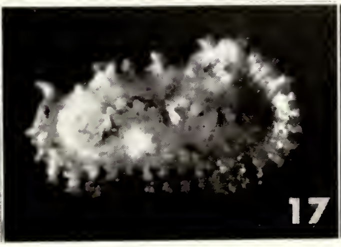

12


13


14


15


16


17

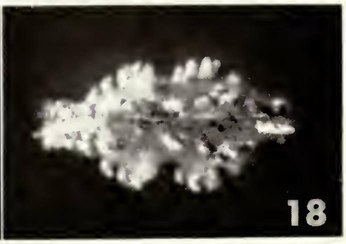

18

PLATE 16

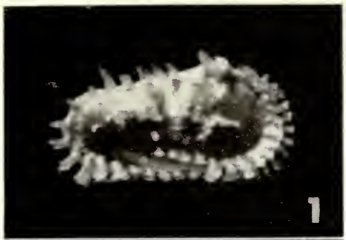
Figs 1, 2. *Cythere clavigera* Brady, lectotype, BM 80.38.59. 1. External view of right valve (× 35), incident light, unstained. 2. Internal view of same right valve in transmitted light (× 45).

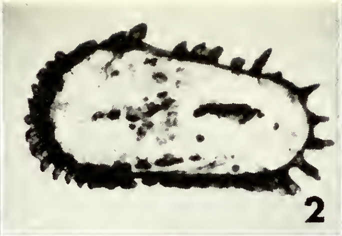
Figs 3–5. *Cythere squalidentata* Brady, lectotype, BM 81.5.29 (× 65), incident light, unstained. 3. External view of whole carapace as seen from left side. 4. External view from right side. 5. External view from top.

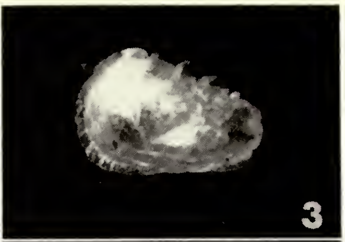
Figs 6–8. *Cythere dictyon* Brady, lectotype, BM 1961.12.4.32. 6. External view of left valve. 7. Internal view of left valve (both × 35), incident light, stained. 8. Enlargement of anteromedian portion of valve in region of subcentral tubercule showing bifurcation anteriorly of posteromedian ridge (× 105).

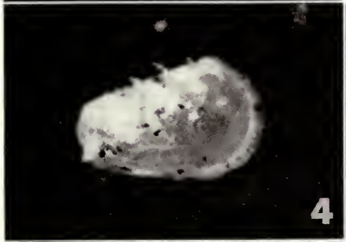
Figs 9, 10. *Cythere arata* Brady, lectotype, BM 80.38.52, penultimate instar (× 60), incident light, stained. 9. External view of right valve. 10. Internal view of right valve.

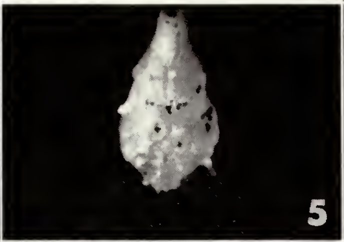
Figs 11–18. *Cythere papuensis* Brady, lectotype, BM 80.38.98. 11, 12. External views of left and right valves of an articulated specimen. 13, 14. Internal views of same right and left valves. 15. Top view of left valve (× 45), incident light, stained. 16. Internal view of anterior hinge element. 17. Muscle scars. 18. Posterior hinge elements of right valve (16, 17, × 145), transmitted light.

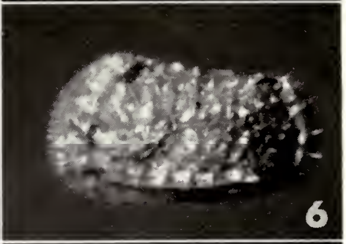

1

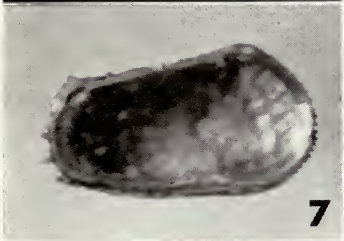

2

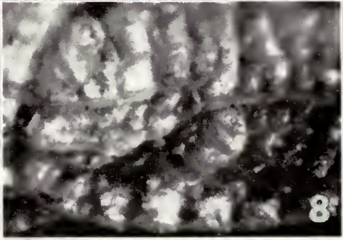

3

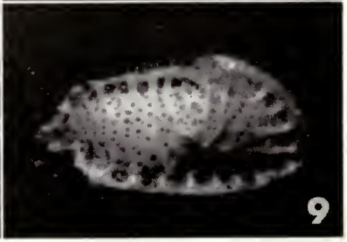

4

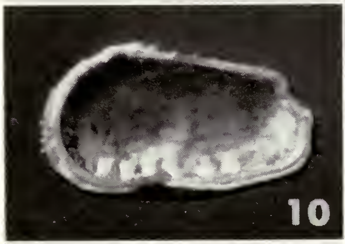

5

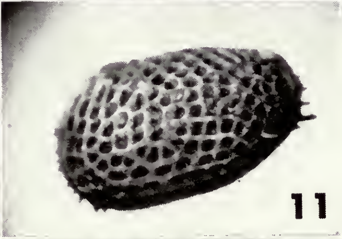

6

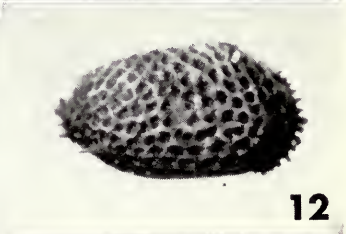

7

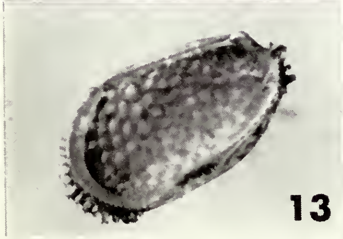

8

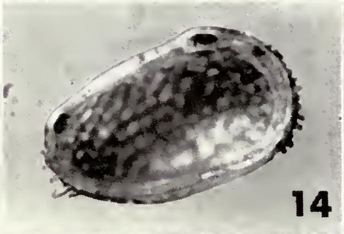

9

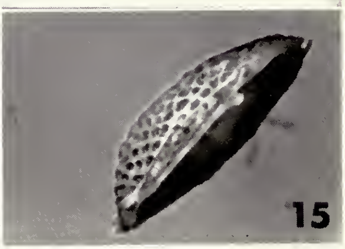

10

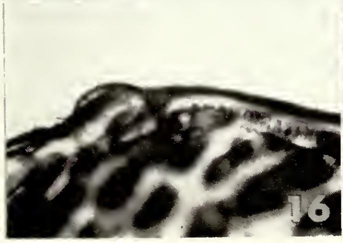

11

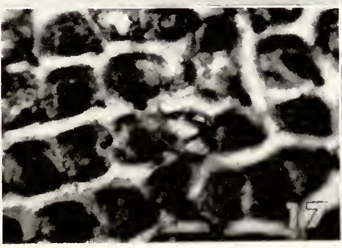

12


13


14


15


16


17

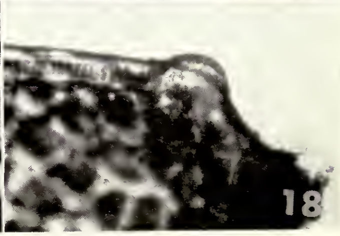

18

PLATE 17

Figs 1–2. *Cythere sulcatoperforata* Brady, lectotype, BM 81.5.30. 1. External lateral view of left valve (× 35), incident light, stained. 2. Internal view of left valve showing merodont hinge and trachyleberid muscle scar (× 25), incident light, stained.

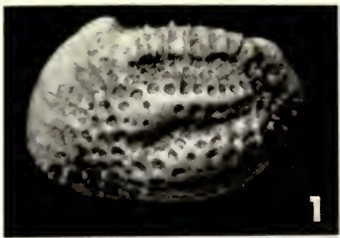
Figs 3–6. *Cythere circumdentata* Brady, lectotype, BM 80.38.58. 3–4. External lateral views of left valve (× 30), incident light, stained, immersed in water and dried. 5. Internal view of left valve showing hinge and marginal area of probable penultimate instar (× 30). 6. Muscle scar (× 80).

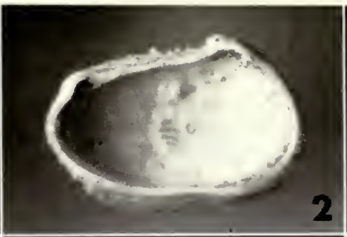
Figs 7–12. *Cythere suhmi* Brady, lectotype, BM 80.38.119 (× 30), incident light, stained. 7–8. External lateral views of left and right valves. 9. Internal view of right valve. 10. External view of left valve. 11. Internal view of left valve. 12. Internal view of right valve (× 35), transmitted light, unstained.

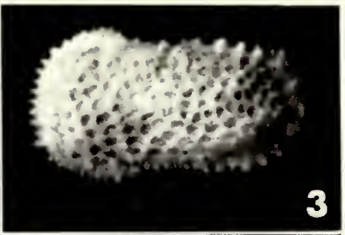
Fig. 13. *Cytherella cribrosa* Brady, lectotype, BM 81.5.66 (× 55), incident light, stained. External lateral view of left valve.

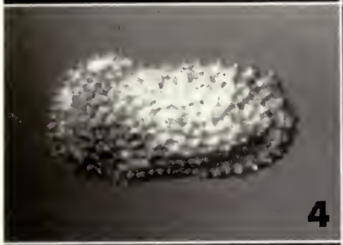
Figs 14, 15. *Cytherella latimarginata* Brady, neotype, BM 81.5.69 (× 75), transmitted light. 14. External lateral view of right valve. 15. External view of left valve.

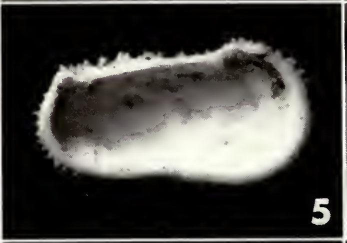
Figs 16–18. *Krithe producta* Brady, BM 80.38.128. 16. External lateral view of left valve (× 40), transmitted light. 17. Muscle scars (× 115). BM 80.38.127 (× 50), incident light. 18. External view of left valve of whole specimen.

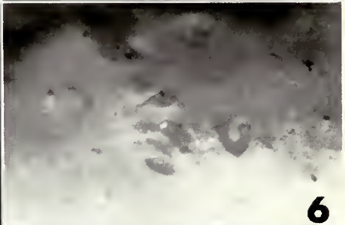

1

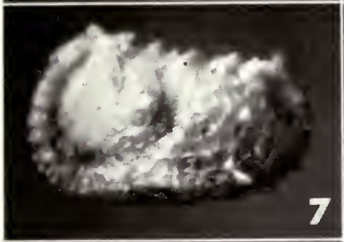

2

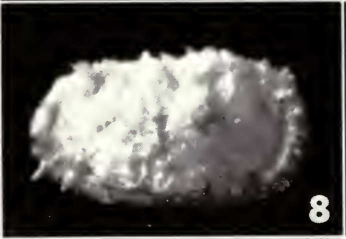

3

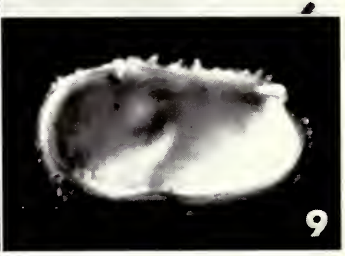

4

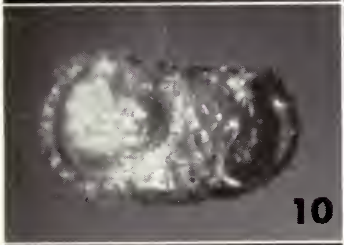

5

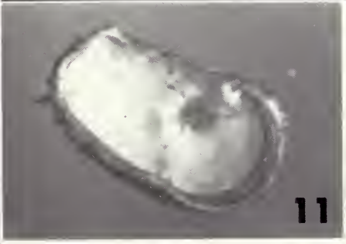

6

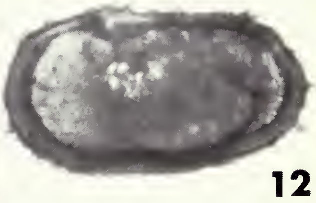

7

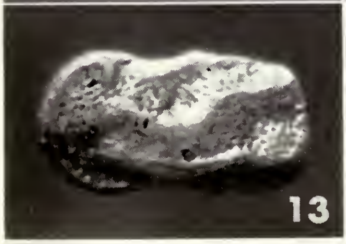

8

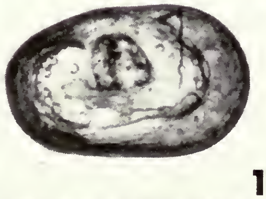

9

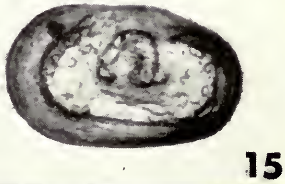

10

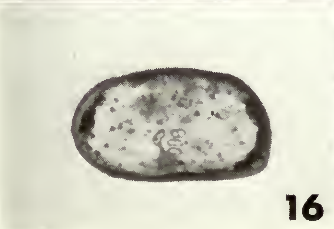

11

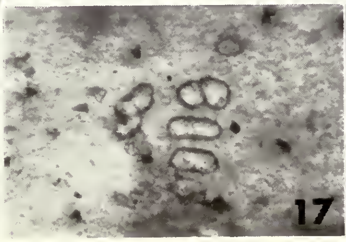

12


13


14


15


16


17

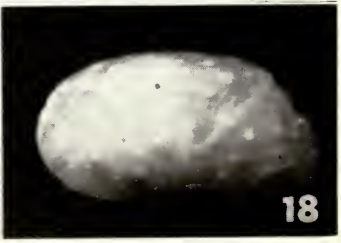

18

PLATE 18

Figs 1, 2. *Krithe hyalina* Brady, lectotype, BM 81.5.34 (× 60), incident light, unstained. 1. External view of left valve. 2. Dorsum of whole carapace.

Figs 3–5. *Krithe tumida* Brady, lectotype, BM 81.5.36 (× 55), incident light, unstained. 3. External view of left valve. 4. Dorsum of whole carapace. 5. Venter of whole carapace.

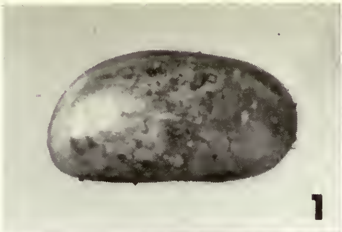
Figs 6–9. *Loxoconcha anomala* Brady, BM 80.38.132. 6, 7. External lateral views of left valve (× 55), incident and transmitted light, stained. 8. Muscle scar region showing adductor scars and aligned subreticulate structure of surface ornament. 9. Lateral view of right valve. (6, 7, 9, × 55 ; 8, × 100), transmitted light.

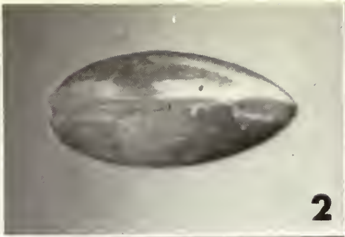
Figs 10–12. *Loxoconcha pumicosa* Brady, lectotype, BM 81.5.37. 10. External view of left valve (× 60), incident light, unstained. 11. Right valve, external view (× 70), transmitted light. 12. Dorsum of whole specimen (× 60).

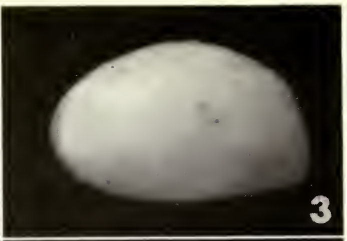
Figs 13, 14. *Loxoconcha africana* Brady, lectotype, BM 80.28.130 (× 50), incident light, stained. 13. External lateral view of right valve. 14. External lateral view of left valve.

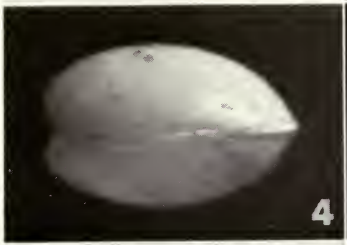
Figs 15, 16. *Loxoconcha subrhomboidea* Brady, lectotype, Hancock Museum (× 70), incident light, stained. 15. External view of left valve showing enlarged row of pits along dorsal side of ventrolateral ridge. 16. Dorsum showing dorsal marginal ridges.

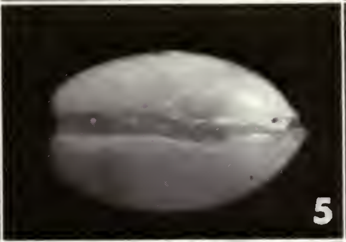
Figs 17, 18. *Loxoconcha australis* Brady, lectotype, BM 80.38.133. 17. External view of left valve (× 95), incident light, stained. 18. Internal view of right valve (× 95), incident light, unstained.

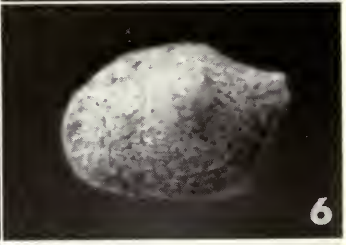

1

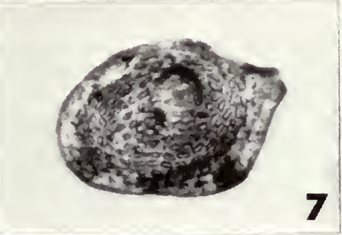

2

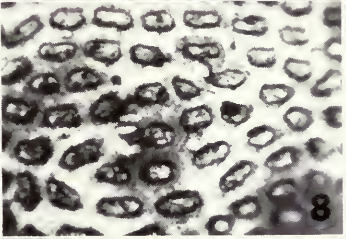

3

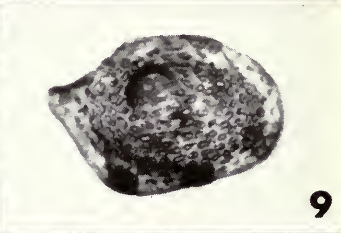

4

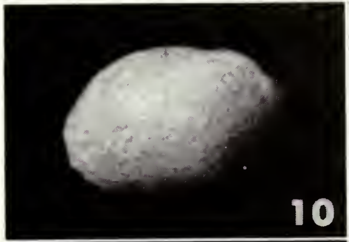

5

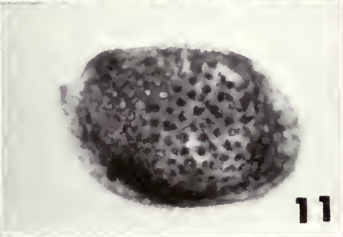

6

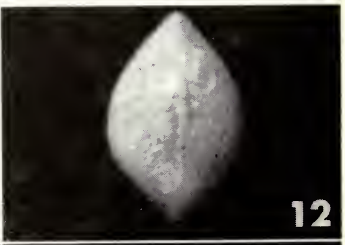

7

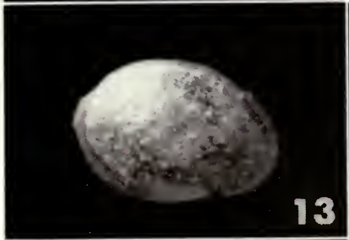

8

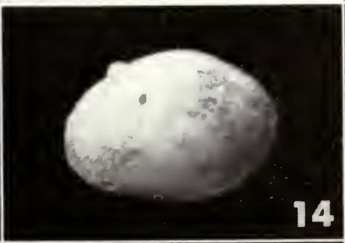

9

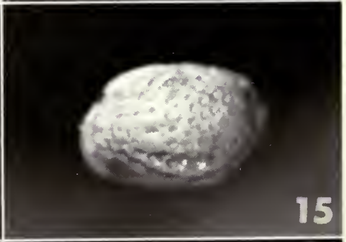

10

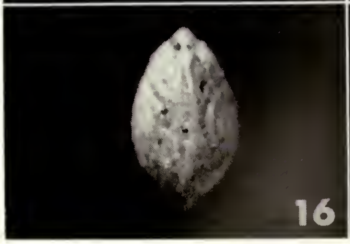

11

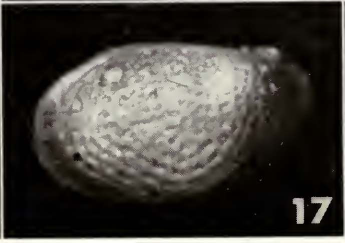

12


13


14


15


16


17

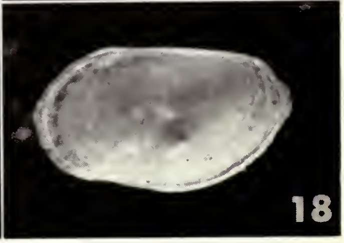

18

PLATE 19

Figs 1–4. *Loxoconcha australis* Brady, lectotype, BM 80.38.133. 1, 2. External lateral views of left valve (× 50), incident and transmitted light. 3. Internal view of left valve (× 65). 4. Muscle scar region showing reticulate surface pattern (× 75) from exterior.

Figs 5, 6. *Loxoconcha honoluliensis* Brady, lectotype, BM 80.38.136 (× 55), incident light, stained. 5. External view of right side of a whole carapace. 6. View from above.

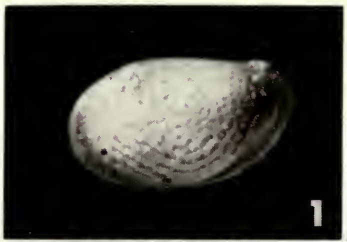
Figs 7–10. *Cytherura clavata* Brady, lectotype, BM 80.38.148 (× 60), incident and transmitted light, stained. 7. External view of left valve. 8. External view of right valve. 9. Internal view of right valve. 10. Internal view of left valve.

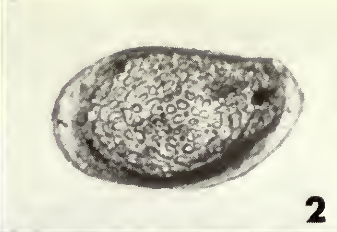
Figs 11, 12. *Xestoleberis foveolata* Brady, lectotype, BM 80.38.141 (× 65), incident light, stained. 11. External view of left valve. 12. Venter of whole carapace.

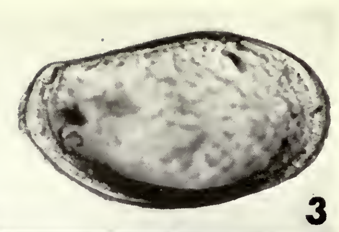
Figs 13, 14. '*Xestoleberis expansa*' Brady, BM 81.5.41 (× 85), incident light, unstained. 13. External view of left valve. 14. Venter of whole carapace.

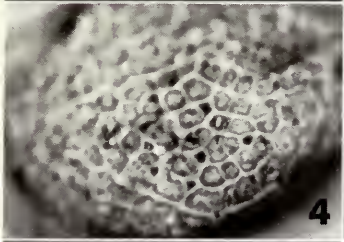
Figs 15, 16. *Xestoleberis africana* Brady, lectotype, BM 81.5.40 (× 80), incident light, unstained. 15. External view of right valve. 16. Dorsum of whole carapace.

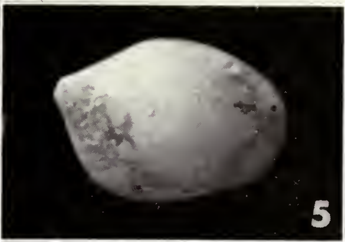
Figs 17, 18. *Xestoleberis granulosa* Brady, lectotype, Hancock Museum (× 60), incident light, unstained. 17. External view of left valve. 18. Venter of whole carapace.

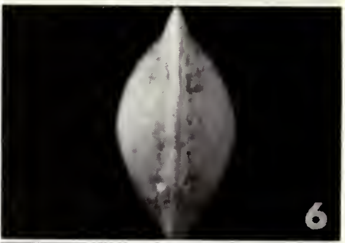

1

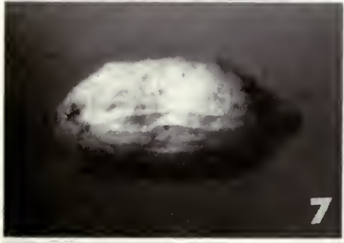

2

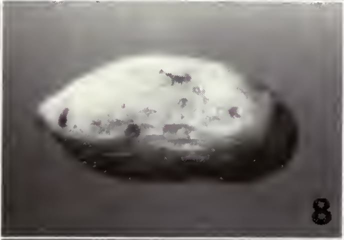

3

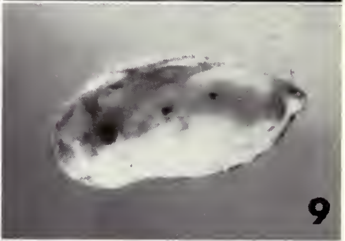

4

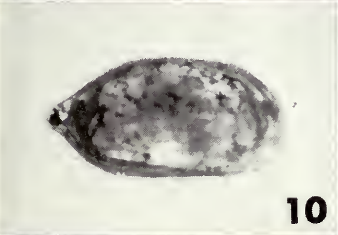

5

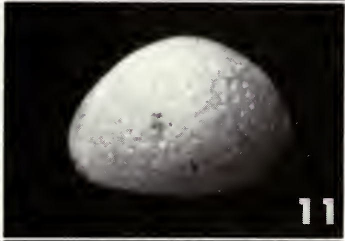

6

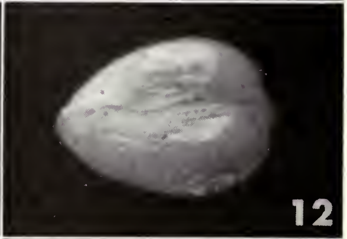

7

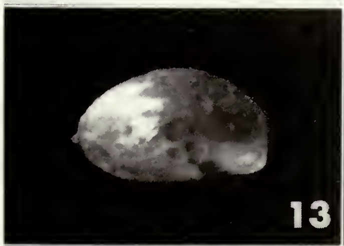

8

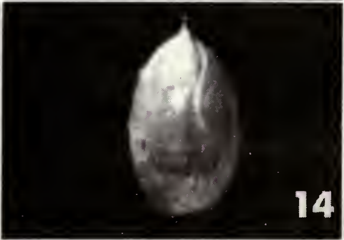

9

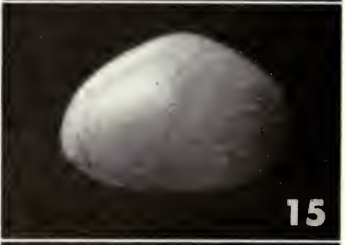

10

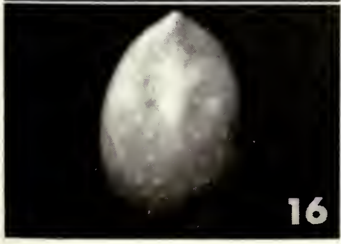

11

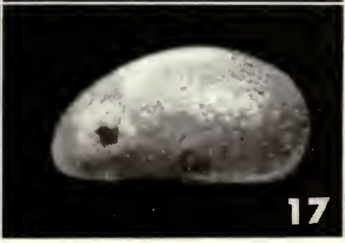

12


13


14


15


16


17

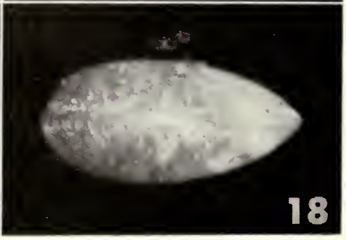

18

PLATE 20

FIGS 1–3. *Aglaia* (?) *pusilla* Brady, lectotype, BM 81.5.2, transmitted light. 1. External lateral view of left valve (× 75). 2. Muscle scars of right valve (× 250). 3. Lateral view of right valve (× 75).

FIGS 4–6. *Aglaia* (?) *meridionalis* Brady, lectotype, BM 1961.12.4.63. 4, 5. External lateral views of left valve (× 80), incident and transmitted light, unstained. 6. Muscle scars (× 190).

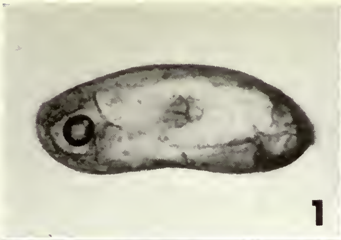
FIGS 7, 8. *Aglaia* (?) *obtusata* Brady, lectotype, BM 80.38.4 (× 90), incident light, unstained. 7. External view of left side of whole carapace. 8. Dorsum of whole carapace.

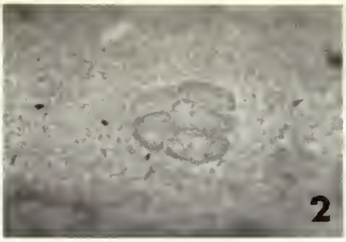
FIGS 9–11. *Xestoleberis setigera* Brady, lectotype, BM 80.38.145. 9. External view of whole carapace as seen from left side. 10. Dorsum (× 40). 11. Venter showing marginal area and radial pore canals (× 50), incident light, unstained.

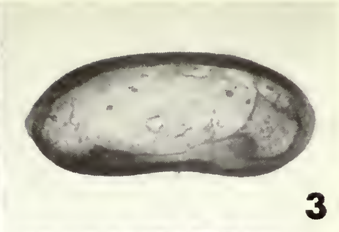
FIGS 12, 13. '*Xestoleberis tumefacta*' Brady, BM 81.5.44 (× 65), incident and transmitted light, stained. External views of broken left valve.

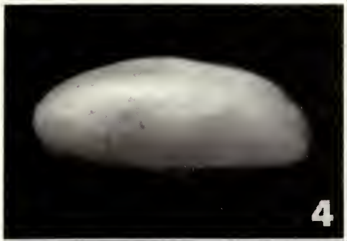
FIGS 14, 15. *Xestoleberis nana* Brady, lectotype, BM 80.38.143 (× 75), transmitted light, unstained. 14. External view of right valve. 15. Internal view of right valve.

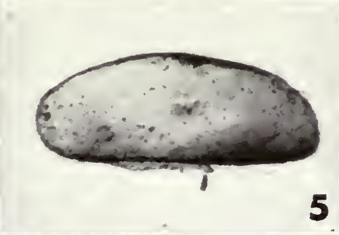
FIGS 16–18. *Xestoleberis variegata* Brady, lectotype, BM 80.38.146 (× 75), incident and transmitted light, unstained. 16. External view of whole carapace as seen from right side. 17. Venter. 18. Dorsum.

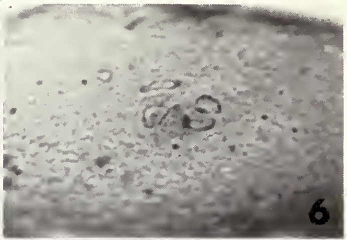

1

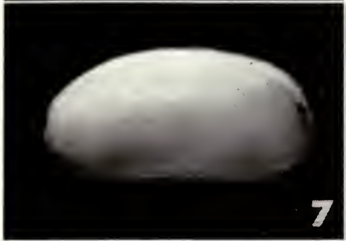

2

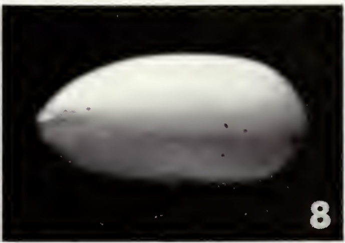

3

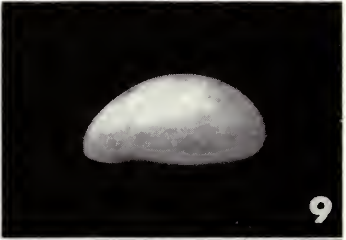

4

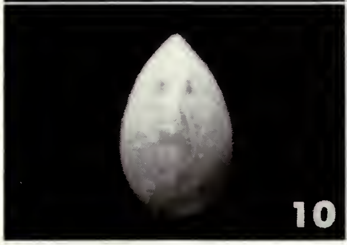

5

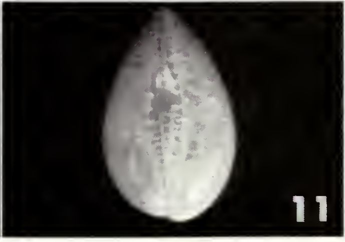

6

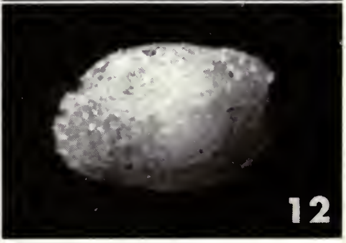

7

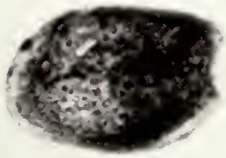

8

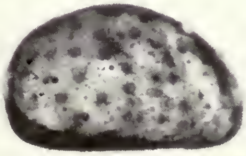

9

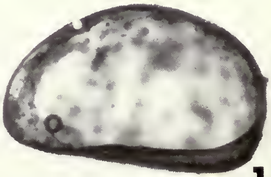

10

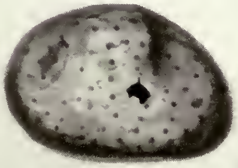

11

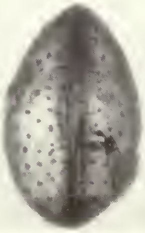

12


13


14


15


16


17

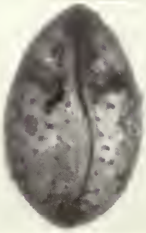

18

PLATE 21

FIG. 1. *Cytherura cryptifera* Brady, Hancock Museum (× 80), incident light, unstained. External lateral view of broken left valve photographed on museum slide.

FIG. 2. *Cytherura cribrosa* Brady, lectotype, BM 80.38.150 (× 70), incident light, stained. External lateral left valve view of complete carapace.

FIGS 3–6. *Cytherura lilljeborgii* Brady, lectotype, BM 80.38.151. 3. External view of whole carapace as seen from left side. 4. Right side (both × 80). 5. Venter. 6. Dorsum (5, 6, × 60, incident light, stained).

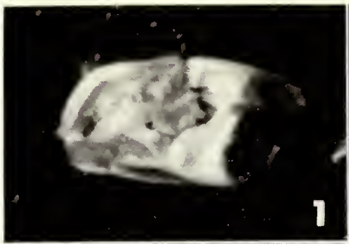
FIGS 7, 8. *Cytherura costellata* Brady, lectotype, BM 80.38.149 (× 60), incident light, stained. 7. External lateral view of right valve. 8. Internal lateral view of right valve.

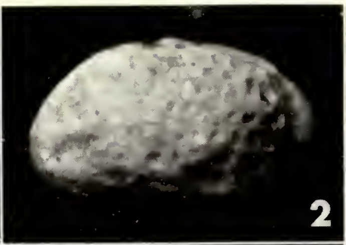
FIGS 9, 10. *Cytherura clausi* Brady, lectotype, BM 81.5.17, incident light, stained. 9. External lateral view of left valve (× 80). 10. Dorsum view of left valve (× 55).

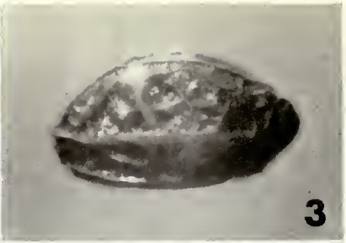
FIGS 11, 12. *Cytherura mucronata* Brady, lectotype, BM 81.5.45 (× 70), incident light, unstained. 11. External lateral view of whole carapace. 12. Dorsum of whole carapace.

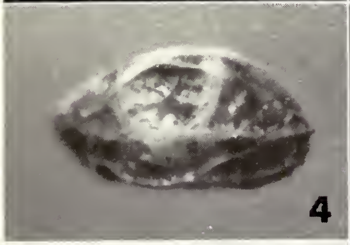
FIG. 13. *Cytherura curvistriata* Brady, lectotype, BM 81.5.46 (× 60), incident light, unstained. External lateral view of complete specimen right valve.

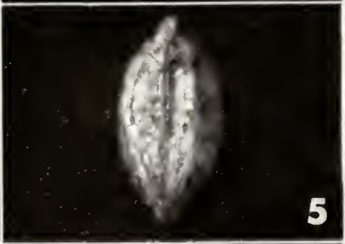
FIGS 14–18. *Cytheropteron scaphoides* Brady, lectotype, BM 80.38.159. 14. External lateral view of right valve. 15. External lateral view of left valve (both of a former single specimen, × 100), transmitted light. 16. Internal view of muscle scar of left valve. 17. Hinge of left valve. 18. Hinge of right valve (both × 270), transmitted light.

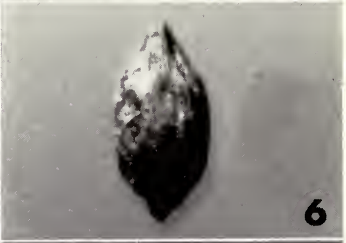

1

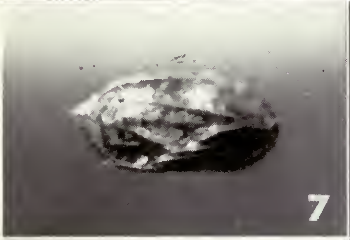

2

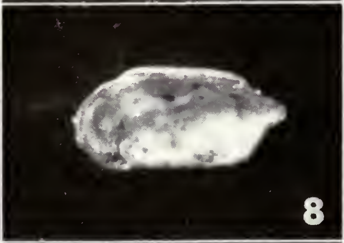

3

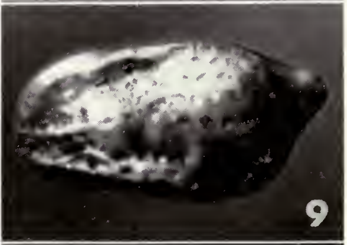

4

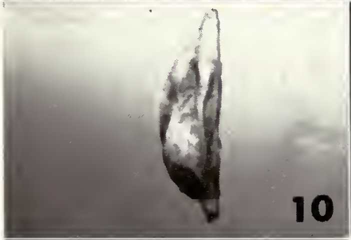

5

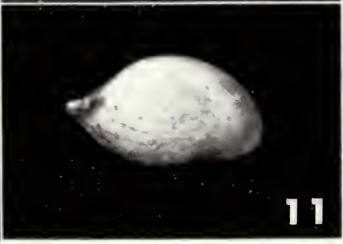

6

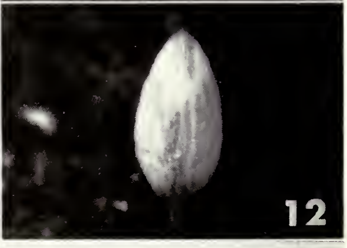

7

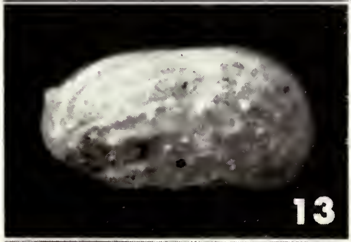

8

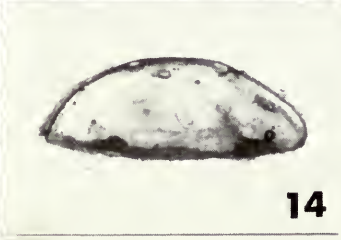

9

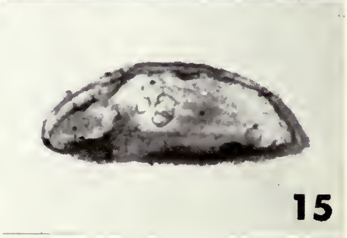

10

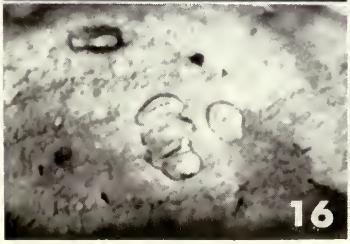

11

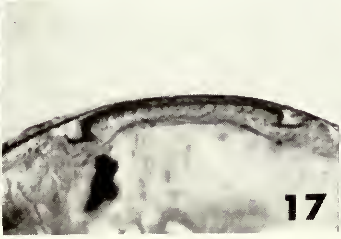

12


13


14


15


16


17

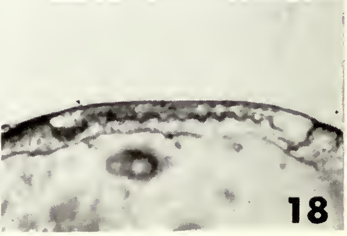

18

PLATE 22

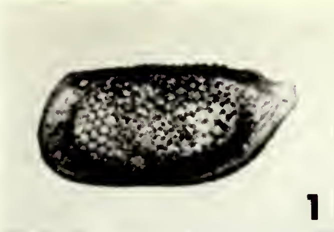
Figs 1–5. *Bythocythere arenacea* Brady, lectotype, BM 81.5.50, transmitted light. 1. Exterior of left valve (× 45). 2. Interior of left valve. 3. Anterior marginal area. 4. Posterior hinge element. 5. Anterior hinge element (3–5, × 150).

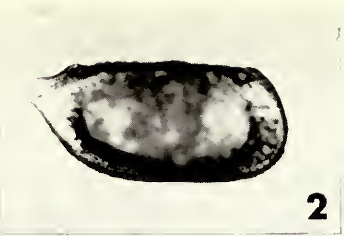
Figs 6–8. *Bythocythere pumilio* Brady, lectotype, BM 81.5.52 (× 40), incident light, stained. 6. Exterior view of whole specimen, left side. 7. View of venter. 8. View of dorsum.

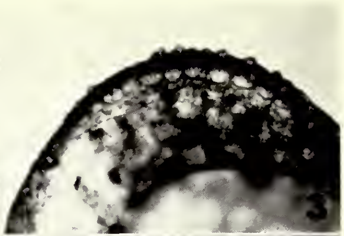
Figs 9–11. '*Bythocythere velifera*' Brady, BM 81.5.53. 9–10. Exterior and interior views of left valve (× 60), transmitted light. 11. View of venter (× 65), incident light, stained.

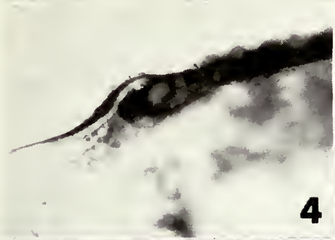
Figs, 12, 13. *Cytheropteron patagoniense* Brady, lectotype, BM 80.38.158 (× 65), incident light, stained. 12. Exterior view of left valve. 13. Interior view of left valve.

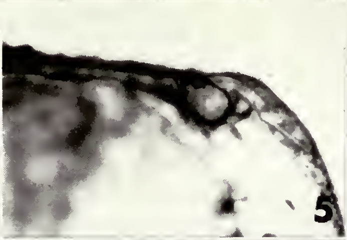
Figs 14–18. *Cytheropteron mucronalatum* Brady, lectotype, BM 80.38,157, all (× 30), incident light, stained. 14, 15. Exterior views of right and left valves. 16, 17. Interior views of right and left valves of a former complete specimen, showing hinge with 'accommodation groove' in left valve and V-shaped frontal scar in right valve. 18. Dorsal view of right valve showing stepped anterior tooth and crenulate posterior tooth.

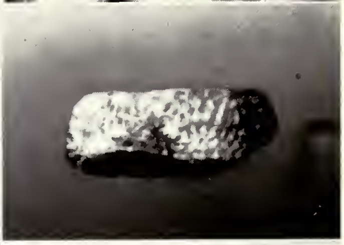

1

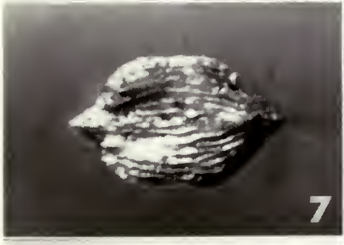

2

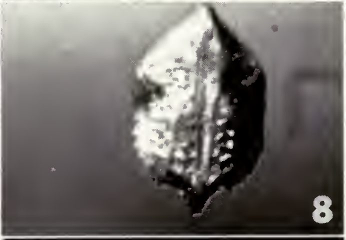

3

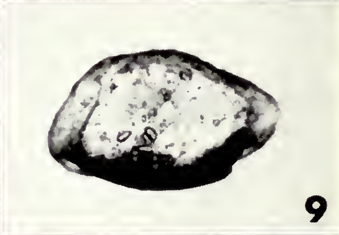

4

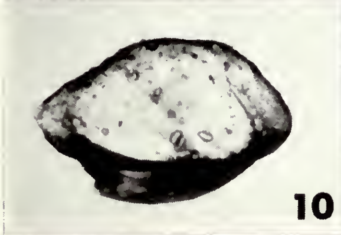

5

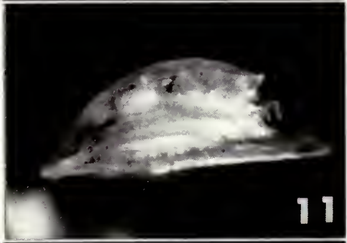


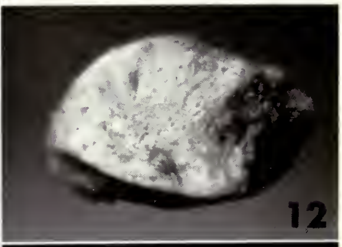

7

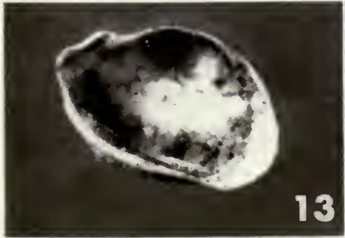

8

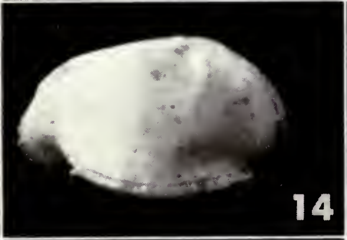

9

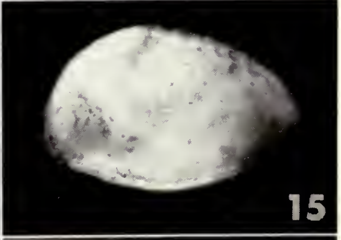

10

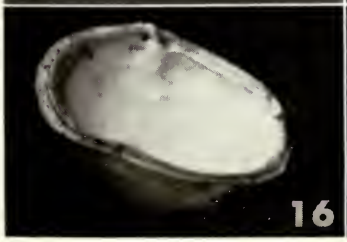

11

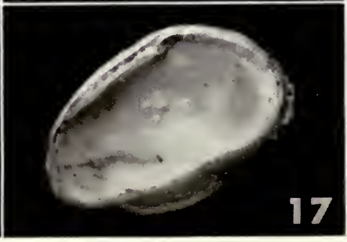

12


13


14


15


16


17

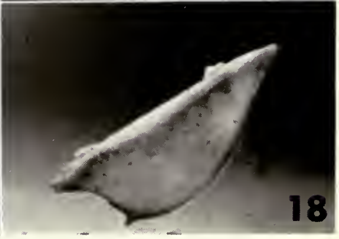

18

PLATE 23

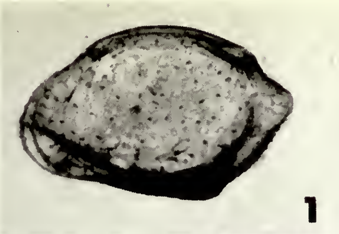
FIGS 1–7. *Cytheropteron assimile* Brady, lectotype, BM 80.38.153, all with transmitted light. 1, 2. External views of left valves (× 55). 3. Dorsal view of posterior hinge element of left valve. 4, 5. Internal views of anterior and posterior hinge elements of right valve. 6, 7. Internal view of anterior and posterior hinge elements of valve (3–7, × 155).

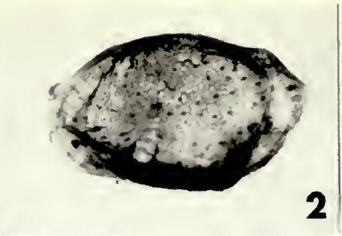
FIG. 8. *Cytheropteron abyssorum* Brady, lectotype, BM 81.5.49 (× 55). Dorsal view of crushed specimen with valves joined.

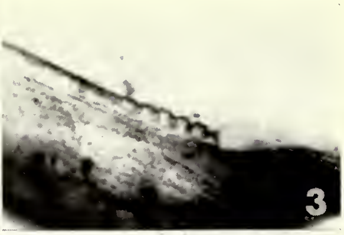
FIGS 9–14. *Cytheropteron wellingtoniense* Brady, lectotype, BM 80.38.160. 9, 10. External views of left and right valves of whole specimen (× 70). 11. Internal view of left valve. 12. Dorsal view of hinge of left valve (× 75). 13. Interior view of anterior hinge element of right valve (× 225). 14. Interior view of muscle scars of right valve (× 250).

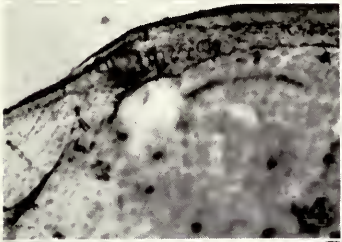
FIGS 15–17. *Cytheropteron* (?) *angustatum* Brady, lectotype, BM 80.38.152, transmitted light. 15, 16. Interior and exterior view of left valve (× 75). 17. Muscle scars (× 130).

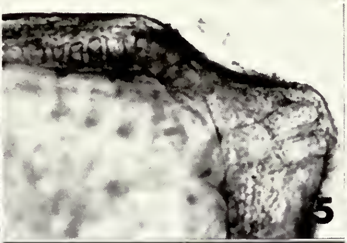
FIG. 18. *Cytheropteron fenestratum* Brady, lectotype, BM 80.38.154–155 (× 40). External view of right valve as seen in black-light illumination.

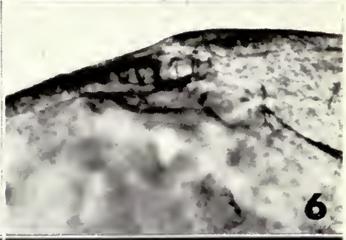

1

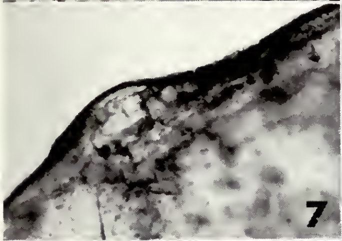

2

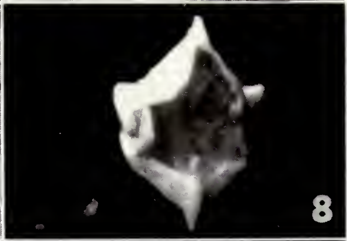

3

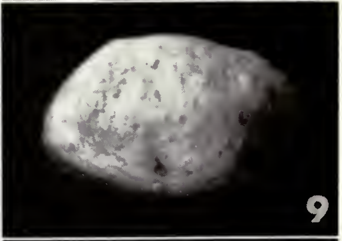

4

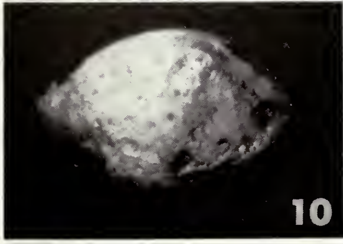

5

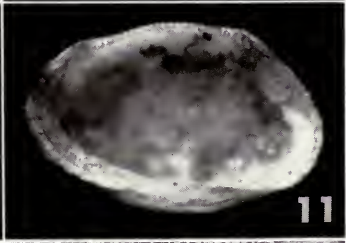

6

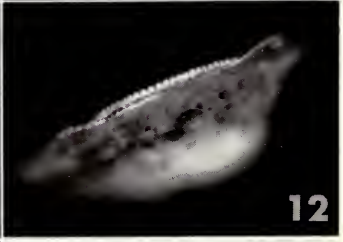

7

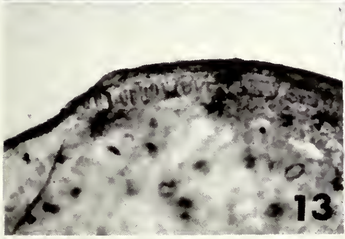

8

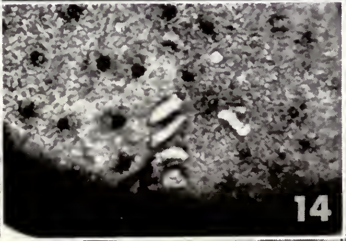

9

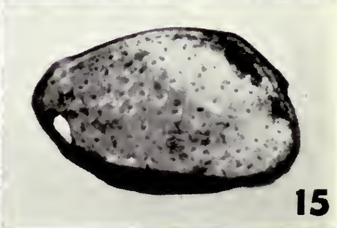

10

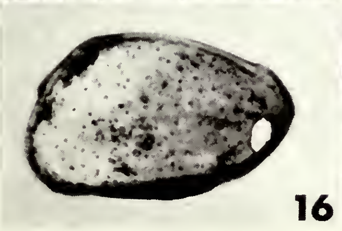

11

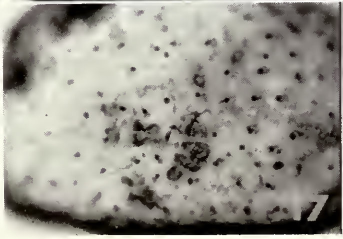

12


13


14


15


16


17

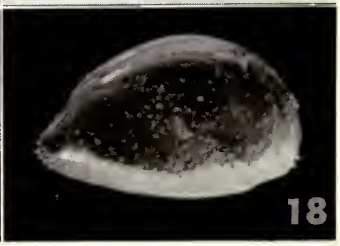

18

PLATE 24

FIGS 1–6. *Cytheropteron fenestratum* Brady, lectotype, BM 80.38.154–155. 1, 2. External lateral views of right valve. 3. External lateral view as seen from above. 4. External lateral view of left valve (all ×40), incident light, unstained. 5. Hinge as seen from above (×80). 6. Posterior element as seen internally in transmitted light showing the tooth and its junctive with confining bars of median groove (×250).

FIGS 7, 8. *Xiphichilus* (?) *arcuatus* Brady, lectotype, BM 81.5.55 (×65), incident light, unstained. 7. External view of left valve. 8. Dorsum of whole carapace.

FIG. 9. *Polycope* (?) *favus* Brady, lectotype, BM 81.5.64 (×75), transmitted light, stained. External view of left valve.

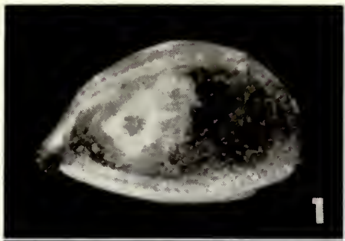
FIG. 10. *Cytherella irregularis* Brady, lectotype, Hancock Museum (×45), photograph taken of specimen on museum slide. External lateral view of damaged left valve.

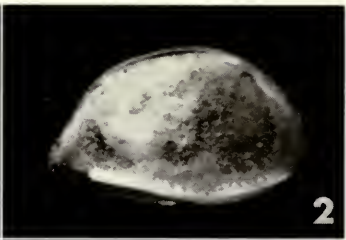
FIGS 11–13. *Cytherella venusta* Brady, lectotype, BM 80.38.180 (×55), incident and transmitted light. 11, 12. External lateral views of left valve. 13. External lateral view of right valve.

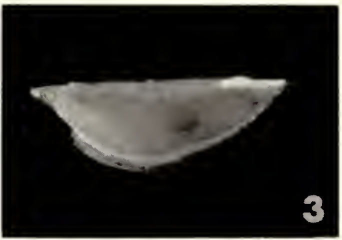
FIG. 14. *Cytherella dromedaria* Brady, BM 81.5.67. External lateral view of left valve.

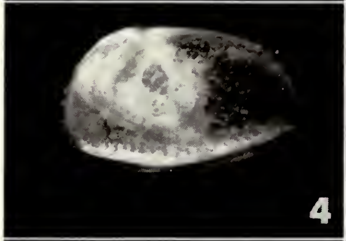
FIGS 15, 16. *Cythere* (?) *serratula* Brady, lectotype, BM 80.38.113 (×35), incident light, stained. External and internal views of right valve.

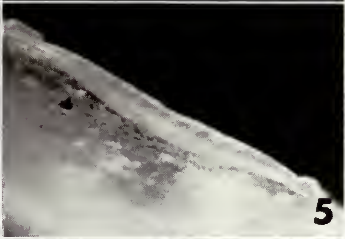
FIGS 17, 18. *Cytherella lata* Brady, lectotype, BM 80.38.172 (×25), incident light, stained. External and internal views of right valve.

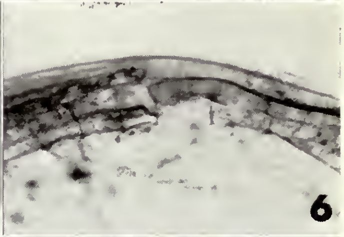

1

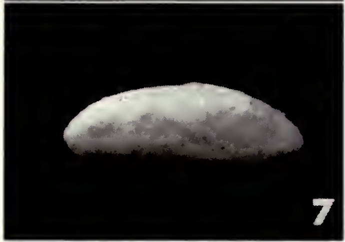

2

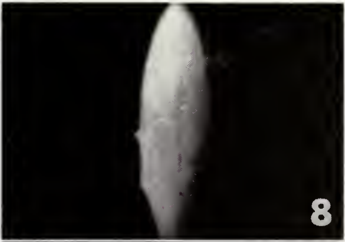

3

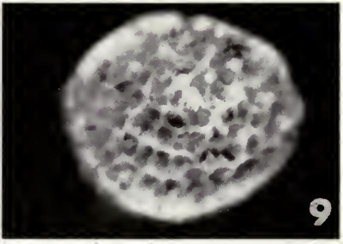

4

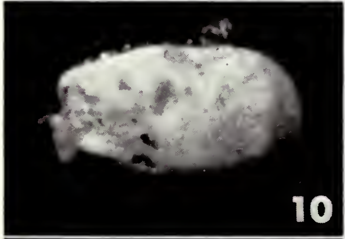

5

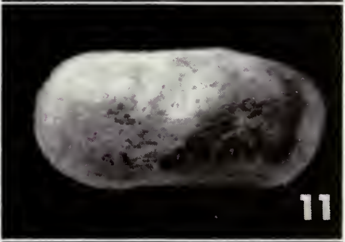

6

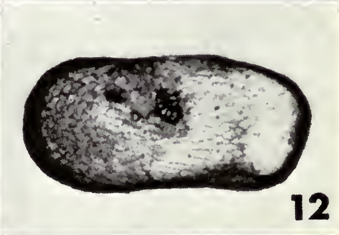

7

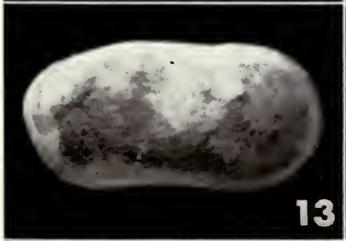

8

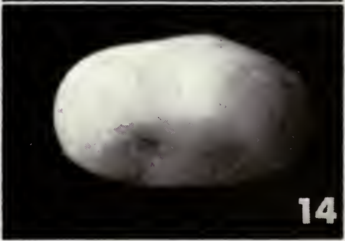

9

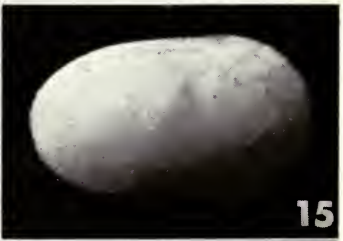

10

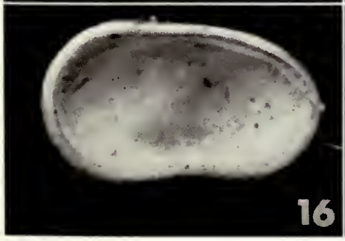

11

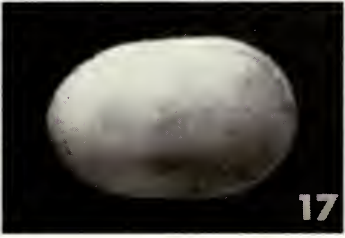

12


13


14


15


16


17

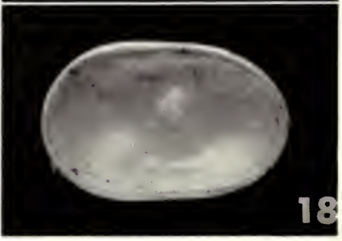

18

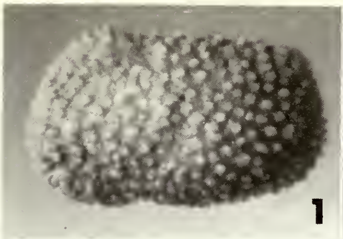
PLATE 25

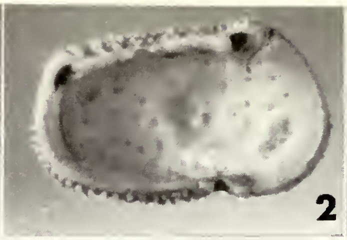
Figs 1, 2. *Cythere melobesioides* Brady, 1869, BM 80.38.92 (×55), incident light, stained. Station 142, off Cape of Good Hope, 150 fathoms. Originally described by Brady, 1869, in *Les Fonds de la Mer*. The specimen photographed is very similar to that illustrated in the Challenger Report (pl. XVIII, figs 1e–g), which he states (p. 162) most closely agrees with the original specimens described from Mauritius in 1869. 1. External lateral view of left valve. 2. Internal lateral view of left valve.

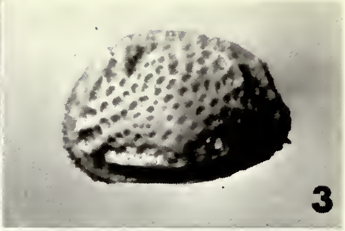
Figs 3–6. *Cythere cymba* Brady, 1869, BM 1961.12.4.44 (×35), incident light, stained. Station 233b, Inland Sea of Japan, 14 fathoms. Described by Brady (1869 : 157) in *Les Fonds de la Mer*, from Hong Kong. 3. Exterior view of a whole carapace as seen from left side. 4. Exterior view of whole carapace as seen from right side. 5. Left lower oblique view of whole carapace. 6. Dorsum.

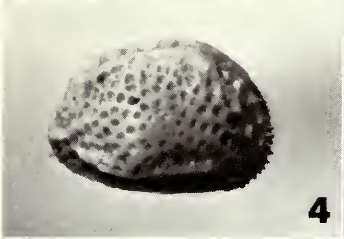
Figs 7–13. *Cythere polytrema* Brady, 1878, BM 80.38.100, off Prince Edward's Island, 50–150 fathoms. Originally described by Brady from fossil specimens from the lower sands and the *Isocardium* bed of the middle sands of Antwerp Crag. This is undoubtedly another species. The present form may be most closely identified to *Cativella bensoni* Neale, 1967. 7. External lateral view of left valve. 8. Internal lateral view of left valve. 9. External lateral view of right valve. 10. Internal lateral view of right valve (all ×45), incident light. 11. Left valve hinge. 12. Right valve hinge. 13. Muscle scars (11–13, ×55).

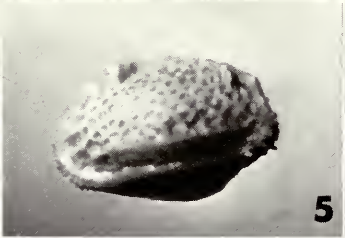
Figs 14–18. *Cythere euplectella* Brady, 1869, BM 80.38.77, station 189, Arafura Sea, 28 fathoms. Originally described by Brady (1869 : 157) in *Les Fonds de la Mer* from Hong Kong. 14, 15. Exterior views of right valve. 16. Interior view of right valve (×65), incident and transmitted light. 17. Muscle scars. 18. Anterior hinge element (both ×120).

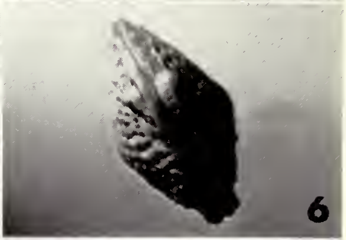

1

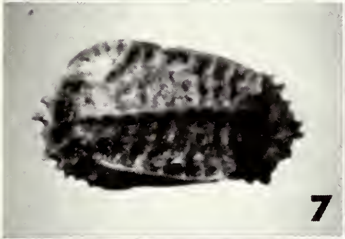

2

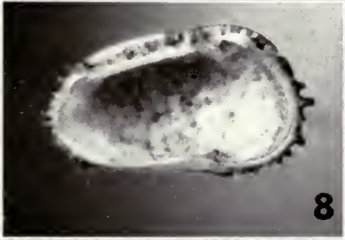

3

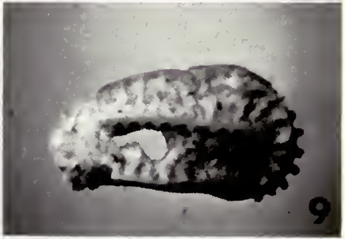

4

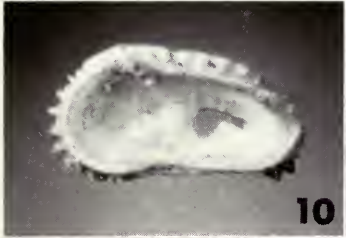

5

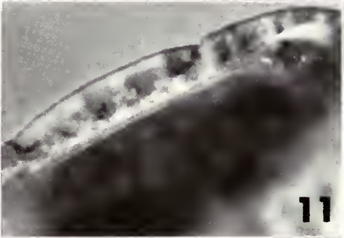

6

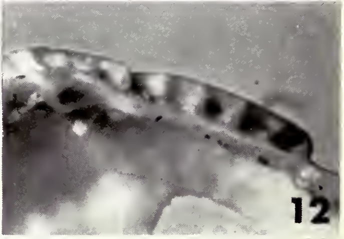

7

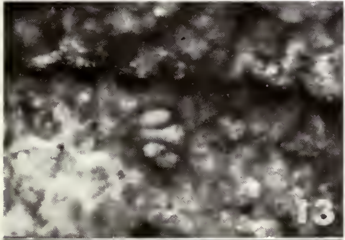

8

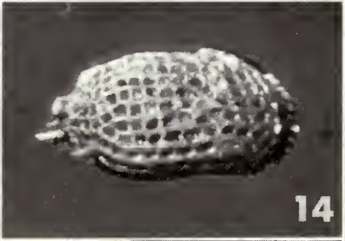

9

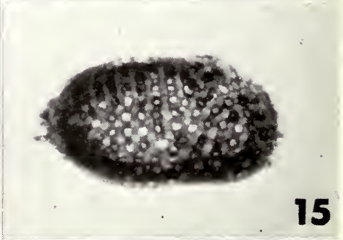

10

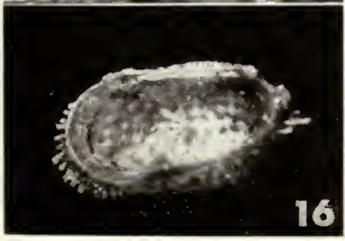

11

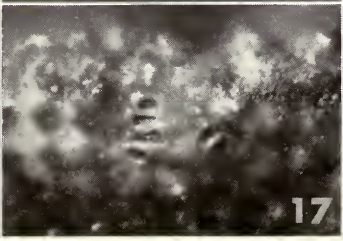

12


13


14


15


16


17

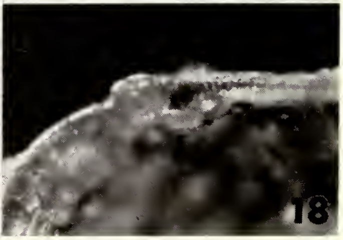

18

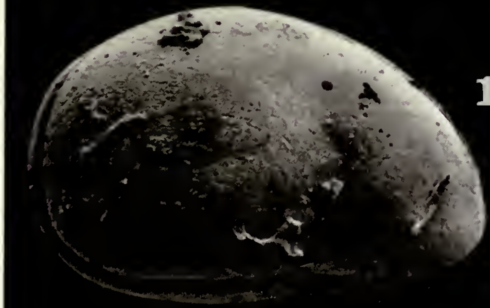
PLATE 26

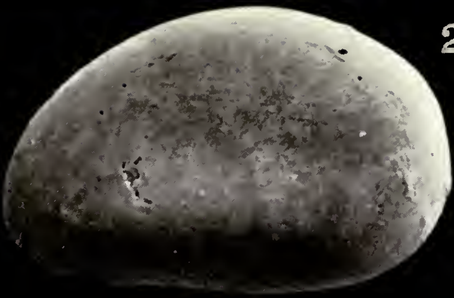
Figs 1–3. *Xestoleberis tumefacta* Brady, neotype, BM 1974.370 (×94). 1. External right lateral view. 2. External left lateral view. 3. Dorsum.

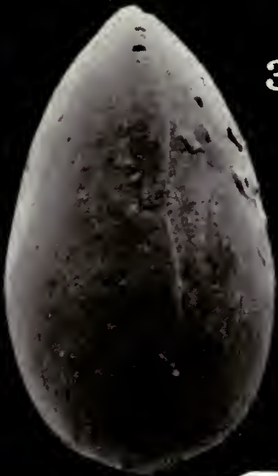
Fig. 4. (?) *Polycope cingulata* Brady, BM 1974.384 (×114). External left lateral view.

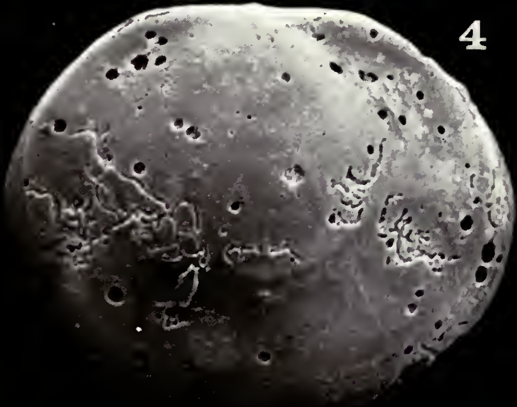
Figs 5, 7. *Cythere cristatella* Brady, BM 80.38.63 (×77). 5. External right lateral view. 7. External left lateral view.

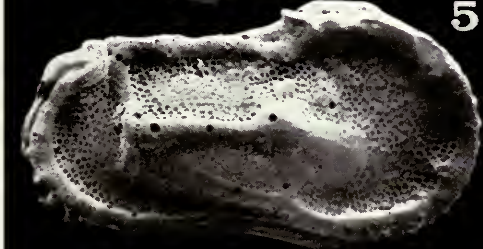
Figs 6, 8. *Cythere scabrocuneata*, Brady, topotype, BM 1974.342 (×64). 6. Internal view left valve. 8. External view left valve.

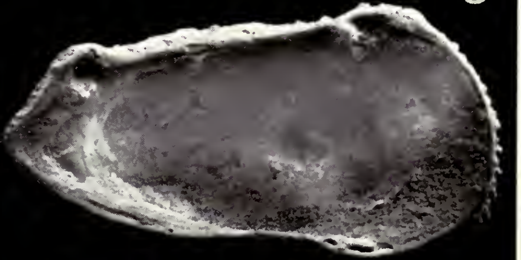

1

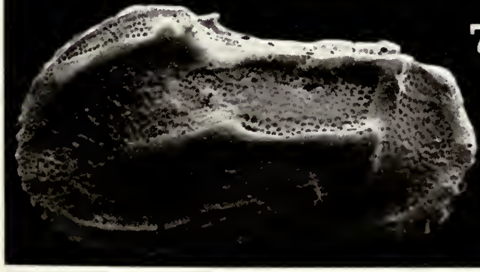

2


3


4


5


6


7

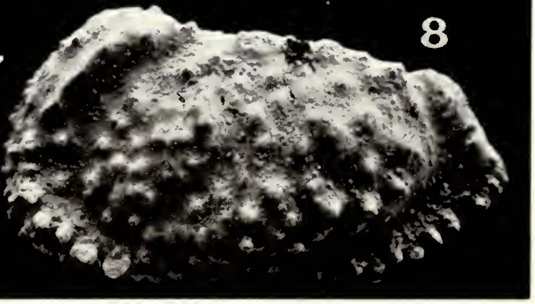

8

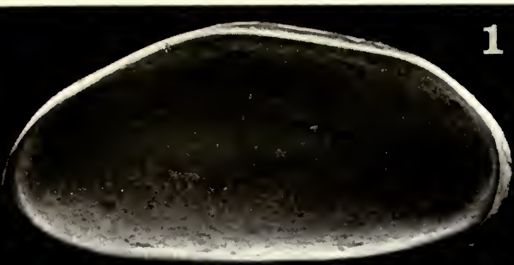
PLATE 27

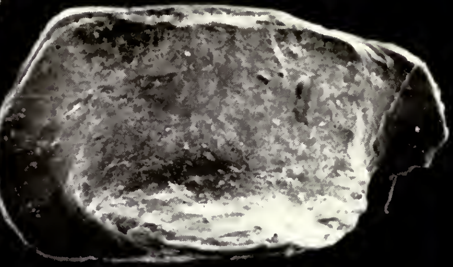
Figs 1, 2. *Argilloecia badia* Brady, topotype, BM 1974.252 A (× 139). 1. Internal view of right valve. 2. External view of right valve.

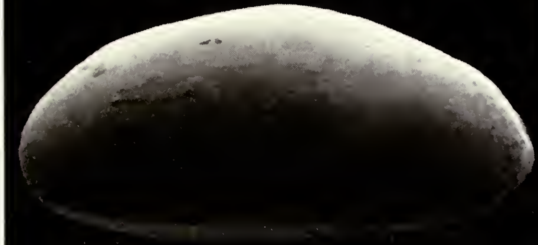
Fig. 3. *Bythocythere velifera* Brady, neotype, BM 1974.381 (× 85). External view of left valve.

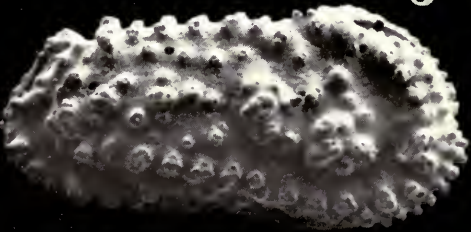
Figs 4–6. *Cythere tetrica* Brady, topotype, BM 1974.338 (× 78). 4. External view of left side of complete carapace. 5. External view of right side of complete carapace. 6. Dorsum of whole carapace.

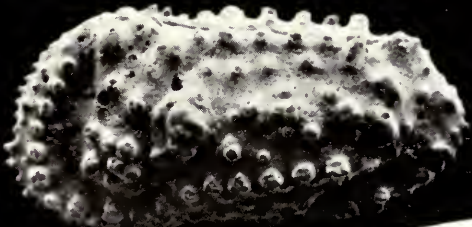
Figs 7–9. *Cythere laganella* Brady, BM 81.5.23 (× 107). 7. Dorsum of whole carapace. 8. External view of right side of complete carapace. 9. External view of left side of carapace.

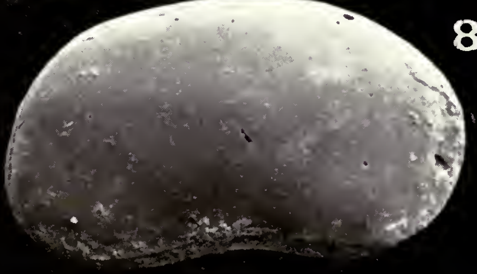

1

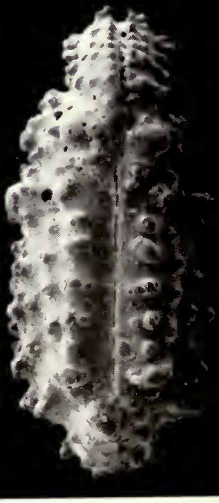

3

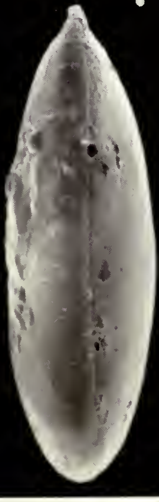

2

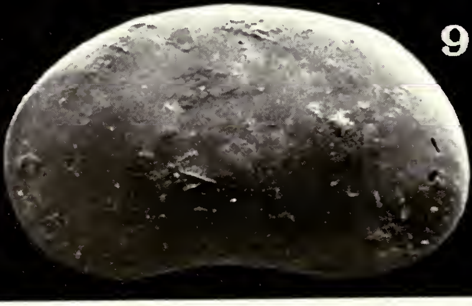

5


4


8


6


7


9

A LIST OF SUPPLEMENTS
TO THE ZOOLOGICAL SERIES
OF THE BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)

1. Kay, E. Alison. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.)
2. Whitehead, P. J. P. The Clupeoid Fishes described by Lacepède, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. Taylor, J. D., Kennedy, W. J. & Hall, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates 77 Text-figures. 1969. £4.50.
4. Haynes, J. R. Cardigan Bay Recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. Pp. 245; 33 Plates, 47 Text-figures. 1973. £10.80.
5. Whitehead, P. J. P. The Clupeoid Fishes of the Guianas. Pp. 227; 72 Text-figures. 1973. £9.70.
6. Greenwood, P. H. The Cichlid Fishes of Lake Victoria, East Africa: the Biology and Evolution of a Species Flock. Pp. 134; 1 Plate, 77 Text-figures. 1974. £3.75. Hardback edition £6.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

SOME TERTIARY AND RECENT CONESCHARELLINIFORM BRYOZOA

USEUM
GENERAL
01 JUN 1976
LIBRARY

P. L. COOK
AND
R. LAGAAIJ

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 6
LONDON: 1976

SOME TERTIARY AND RECENT CONESCHARELLINIFORM BRYOZOA

B.M.S. MUSEUM
GENERAL
01 JUN 1976
LIBRARY
NATURAL HISTORY

BY
PATRICIA L. COOK
British Museum (Natural History)
AND
ROBERT LAGAAIJ
Shell International Petroleum

Pp. 317–376 ; 8 *Plates* ; 7 *Text-figures* ; 3 *Maps*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 29 No. 6
LONDON : 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 29, *No.* 6, *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Zool.)

ISSN 0007-1498

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 27 *May* 1976 *Price* £5·40

SOME TERTIARY AND RECENT CONESCHARELLINIFORM BRYOZOA

By PATRICIA L. COOK & ROBERT LAGAAIJ[1]

CONTENTS

	Page
Synopsis	319
Introduction	320
Terminology	321
Structure and budding	323
Orientation of the colony, rootlets and early astogeny	327
Comparison of astogenetic series	331
Coding of characters and results of polythetic clustering	333
Evolutionary trends in morphology	342
Ecology and palaeoecology	343
Distribution in time and space	346
Conclusions	348
Descriptions of species	349
Family Orbituliporidae	349
Genus *Batopora*	349
Batopora stoliczkai Reuss	352
Batopora grandis sp. nov.	353
Batopora asterizans sp. nov.	354
Genus *Lacrimula*	355
Lacrimula burrowsi Cook	356
Lacrimula visakhensis Rao & Rao	357
Lacrimula perfecta (Accordi)	358
Lacrimula borealis sp. nov.	360
Lacrimula asymmetrica sp. nov.	361
Lacrimula grunaui sp. nov.	363
Lacrimula similis sp. nov.	363
Genus *Atactoporidra*	365
Atactoporidra bredaniana (Morren)	365
Acknowledgements	367
Summaries in French and German	367
Appendices	368
References	374

SYNOPSIS

The characters of conescharelliniform and orbituliporiform colonies of Bryozoa, and the occurrence in both groups of two types of astogeny, 'normal' and 'frontal', are described. The genera *Conescharellina* and *Trochosodon* are known to be anchored to their substrata by rootlets. They are compared with the genera *Batopora*, *Lacrimula* and *Atactoporidra*. A hypothetical model for the primary colony development of these genera is suggested. The characters and distribution in time and space of the genera *Batopora*, *Lacrimula*, *Atactoporidra* and *Conescharellina* are discussed, and the available information on their ecology and palaeoecology is

---

[1] This paper was in the final stages of preparation at Dr Lagaaij's death in January, 1975. The sections on the results of polythetic clustering and the conclusions had been discussed but were not then completed; they therefore represent principally my own interpretations. P. L. Cook

recorded. Full descriptions are given of three species of *Batopora*, two of which are considered to be new, and of seven species of *Lacrimula*, four of which are considered to be new. The combined effects of genetics and environment outweigh microenvironmental influences within the colony. Integration within colonies is considerable, and is demonstrated by the interzooidal communications, astogenetic zonation and polymorphism. The specialized mode of life allows palaeoecological inferences to be made as to depth and type of sea-bottom from the Eocene to the Recent.

INTRODUCTION

MARINE cheilostomatous Bryozoa have evolved colony forms capable of inhabiting many environments. Members of the ascophoran families Orbituliporidae and Conescharellinidae particularly appear to be adapted to conditions unsuitable for many other forms. The members of the two families are closely similar in many characters, not least in the possession of a form of astogeny which may be unique among Bryozoa (see below). Both families exhibit parallel groups of genera with distinct colony forms, and it must be stressed that those which are here considered to be 'orbituliporiform' colonies are found both in the Orbituliporidae (e.g. some species of *Orbitulipora*) and in the Conescharellinidae (e.g. *Flabellopora*). Conversely, 'conescharelliniform' genera are found in the Conescharellinidae (e.g. *Conescharellina*) and in the Orbituliporidae (e.g. *Batopora*). Other genera exhibiting similar colony forms have no close systematic relationship with these families and have an entirely different astogeny (see below). For example, 'orbituliporiform' colonies occur in *Lanceopora* and 'conescharelliniform' colonies in *Fedora*.

This paper is principally concerned with the colony structure, diversity, distribution and relationships of three conescharelliniform genera, *Batopora* (Eocene to Recent), *Lacrimula* (Eocene to Recent) and *Atactoporidra* (Eocene to Oligocene). The relationships and distribution of a fourth genus-group, comprising some representatives of the genera *Trochosodon* and *Conescharellina*, are briefly compared.

Conescharelliniform colonies are small, rarely reaching 8 mm in height or diameter. They are conical, usually with no large basal concavity, and apparently without substratum. The ancestrula or ancestrular complex is concealed by secondary kenozooidal or extrazooidal tissue in later astogenetic and ontogenetic stages. Orbituliporiform colonies are frequently larger, often reaching 20–30 mm in height or diameter. They are actually or apparently bilaminar, and may be disc-shaped, sagittate or trilobate. One of the disadvantages in defining colony form in terms derived from names of genera which illustrate a distinct type of structure is that the terms themselves may begin to carry with them a systematic connotation. The term 'lunulitiform' (from *Lunulites*) is, however, now generally used for cup-shaped or conical colonies which are free-living, and which at some stage in their astogeny have a basal cavity. Although the overall form of these colonies is similar, the budding pattern, microstructure and interrelationships of polymorphs are totally dissimilar. Unrelated genera included in this grouping are, for example, *Lunulites*, *Cupuladria*, *Selenaria* and *Cyttaridium*.

Conescharelliniform and orbituliporiform colonies have, in common with lunulitiform colonies, an association with fairly calm to calm, often deeper shelf waters, and a soft unstable sea-bottom, with the concomitant problems to the bryozoan of deposition and restricted availability of substratum for settlement of larvae. Unlike lunulitiform colonies, orbituliporiform and conescharelliniform colonies may inhabit abyssal depths and have been observed, or may be inferred, to possess cuticular rootlets as an essential part of the colony structure.

The astogeny of both types of colony may be similar to that found in encrusting cheilostome species ; i.e. new zooid buds arise from the distal or distal-lateral walls of existing zooids, forming linear series of increasing astogenetic age in the direction leading away from the ancestrular area ('normal astogeny'). In other colonies of both groups new zooids are budded entirely from the frontal walls of existing zooids in a succession which is described in detail below (p. 324) as 'frontal astogeny'. Conescharelliniform and orbituliporiform genera exhibiting these forms of growth include :

Conescharelliniform colonies	'frontal astogeny'	*Conescharellina, Trochosodon, Batopora, Lacrimula, Atactoporidra, Fedorella*
	'normal astogeny'	*Fedora, Kionidella, Mamillopora*
Orbituliporiform colonies	'frontal astogeny'	*Orbitulipora, Flabellopora, Zeuglopora*
	'normal astogeny'	*Lanceopora*

TERMINOLOGY

Classical terms in bryozoan morphology have rather wide definitions, but in practice some have been found to be satisfactory. There are considerable difficulties, however, in applying these terms to the genera discussed here. These stem in part from the peculiar structure of the colonies themselves, and in part from the fact that their orientation in life is unknown.

Distal and basal walls as such do not exist in these colonies, and the classical 'distal' direction of the astogenetic process is apparently 'proximal'. The orientation of the colony in relation to the substratum is not known from direct observation. The term 'distal' usually refers to that direction, and by morphological analogy, to those zooidal walls, and parts of the whole colony, which are astogenetically 'away from' the ancestrular area. Similarly the conventional representation of conical, lunulitiform colonies assumes that the geometric apex of the cone is uppermost, as in these colonies the basal walls are, by direct observation of living forms, directed downwards (see Cook, 1963 ; Greeley, 1967). The terms used here are defined below (see Figs 1 and 2).

Adapical – directed toward the apical region of the colony (the classically 'distal' part of the orifice is adapical).

Antapical – directed away from the apical region of the colony.

Apical region – the region of the colony in which the ancestrula and primary zooids may be observed or inferred to occur.

Concealed frontal wall – that part of the frontal wall of each zooid which, except in the proliferal region, is hidden from view. Primary series of frontal buds originate from this part of the wall.

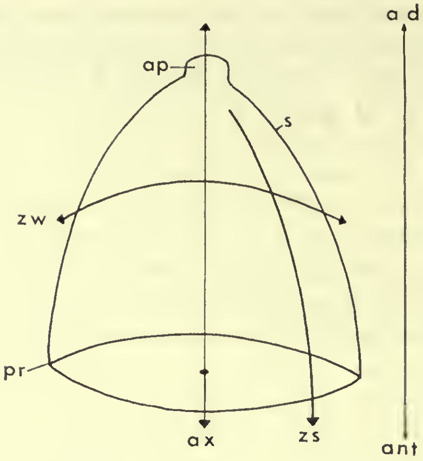


FIG. 1. Terms used in describing conescharelliniform colonies with 'frontal' budding. Note that the colony orientation in life is *not* known. *ad*, adapical direction ; *ant*, antapical direction ; *ap*, apical region ; *ax*, colony axis ; *pr*, proliferal region ; *s*, colony surface ; *zs*, zooid series ; *zw*, zooid whorl.

Exposed frontal wall – that part of the frontal wall of each zooid which surrounds the orifice and which contributes to the exposed surface of the colony between its geometrical apex and its geometrical base. Secondary series of frontal buds may originate from this part of the wall.

Proliferal region – the region of the colony in which the most recently formed primary zooid buds (i.e. those of the primary zone of astogenetic change) may be observed or inferred to occur.

Rootlets – long cuticular kenozooids or zooidal extensions arising from specific positions in a colony, actually or hypothetically functioning as anchoring structures.

Rootlet pores – small areas, which may be kenozooids derived by frontal budding from frontal septulae, from which rootlets may be observed or be inferred to originate.

Abbreviations used:

AxL	axial length of colony
Prl	proliferal region width of colony
Lfw	length of exposed frontal wall
lfw	width of exposed frontal wall
Lo	orifice length
lo	orifice width
Lov	ovicell length
lov	ovicell width
Lt	length of apical tube
BM	British Museum (Natural History)
NMV	Naturhistorisches Museum, Vienna
USNM	United States National Museum

STRUCTURE AND BUDDING

Apparent reversal of the orientation of the zooidal orifice occurs in two distinct forms in Bryozoa. In the Inversiulidae the operculum opens in a distal direction, but all other zooidal relationships appear to be normal (see Harmer, 1957 : 956). In the Conescharellinidae and Orbituliporidae the whole zooidal orientation is apparently reversed in relationship to the direction of budding of the colony. The classically 'distal' part of the orifice is thus directed towards and not away from the ancestrular region.

Hypothetical models illustrating the methods involved in this reversal have frequently been made in the past, two of the most recent being those of Silén (1947) and Harmer (1957). They have been based on the assumption that budding in Bryozoa is primarily a function of the distal and/or lateral zooidal body walls. In the Cheilostomata, the astogeny of the great majority of species consists of the production of a primary uncalcified bud by the expansion of cuticle and underlying epidermis distally from an existing zooid. The bud usually proceeds to secrete calcified basal and lateral walls, and becomes limited distally by the growth of a transverse distal wall. Coelomic connection between and among zooids is through septulae in the lateral and distal walls.

Recently, studies have been made on another type of astogenetic series in the Ascophora, the formation of 'frontal' buds (see Banta, 1972). Hastings (1964), in

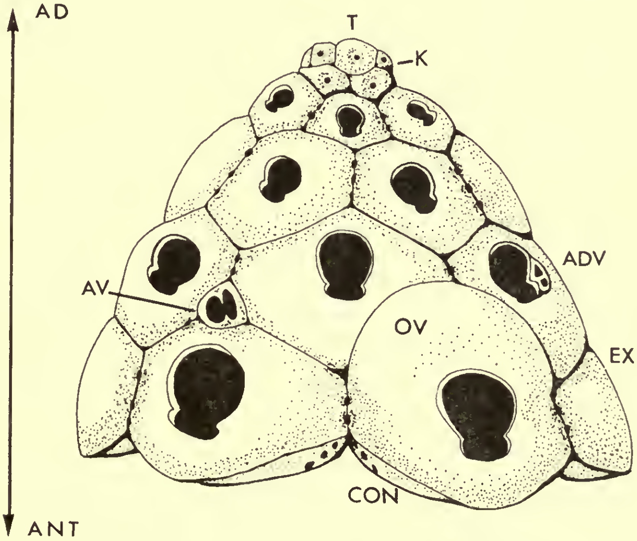


FIG. 2. Generalized morphology of a conescharelliniform colony with one zone of astogenetic change. Colony has four zooid whorls and six zooid series budded alternately. Note condyles of zooid orifices, marginal pores, avicularia and ovicells. AD, adapical direction ; ANT, antapical direction ; CON, concealed frontal wall ; EXP, exposed frontal wall ; T, position of internal or external apical tube ; K, apical area of kenozooids, and/or closed zooids or extrazooidal tissue ; AV, interzooidal avicularium ; ADV, adventitious avicularium ; OV, ovicell.

describing the colony structure of *Reginella doliaris* (Maplestone), a cribrimorph species with a free-living conical colony form, postulated a kind of frontal budding, and compared the astogeny with that of *Conescharellina*.

Although there may be several methods by which these frontal buds are formed, the sequence of development is basically as follows. There is an expansion of cuticle and underlying epidermis above the calcified frontal wall of an existing zooid. Coelomic connection is provided by frontal septulae, which seem to be represented by some or all of the marginal pores. The buds so produced have no cuticle basally, and some do not appear to have lateral walls. Marginal septulae are present. Some colonies may show long series of frontal buds which develop in a plane at right angles to that of the primary growth (see also Boardman, Cheetham & Cook, 1969, fig. 5). Other colonies may produce small groups of frontal buds, which then proceed to bud distally and laterally, forming a secondary layer of zooids above and parallel to that of the primary growth (similar to an 'overgrowth' of Boardman *et al.*, 1969, fig. 6). Zooids of this kind of secondary layer may therefore be distinguished from frontally budded layers by the possession of a basal wall and basal cuticle.

In the Conescharellinidae and Orbituliporidae normal distal or distal-lateral budding appears to have been completely abandoned in favour of frontal budding. Each zooid may be considered to have a calcified frontal wall which has extended at the expense of the distal, lateral and basal walls. At the same time, the frontal wall has become divided into two elements. The first element is a flat or inflated, often hexagonal portion which represents the projection of the geometrical base of a cone at the surface of the colony. The second portion consists of part of the remainder of the cone. The 'basal' wall of each zooid completes the cone, but this is composed of the frontal wall, or walls, of the parent zooid or zooids (see Figs 2 and 3). Marginal pores, which are inferred to be septulae, are placed round the periphery of the hexagonal portion of the frontal wall and in two converging rows on its remaining surface ('exposed' and 'concealed' frontal wall elements, see p. 321). The next generation of frontal buds is produced either directly from one or from between two existing zooids, arising in a line extending along the 'concealed' part of the frontal wall toward the centre of the colony, and thus including two series of marginal pores. As the bud enlarges it completes the conical shape, and the enlarged frontal wall calcifies, the geometrical base of the zooid cone again forming the hexagonal exposed frontal wall at the surface of the colony, and surrounding a centrally placed orifice.

In both families, buds are produced in direct or in alternating series, i.e. only one, or two to three zooids of the previous generation contribute to the next generation. In the Conescharellinidae the type of budding is usually direct and specific. It was illustrated by Harmer (1957) for most species of *Conescharellina* and *Trochosodon* (but *C. ovalis*, p. 743, buds in alternating series). In the Orbituliporidae, most species bud in alternating series, and there is a good deal of intracolony variation. Even in zooids budded directly, there may be a variable contribution from other zooids, potentially at least, as their marginal pores are incorporated beneath the frontal wall of the new bud. Some colonies, for example the largest of *Lacrimula burrowsi*, show an initial secondary zone of alternating budding, which, as it gives rise to a few intercalary series of zooids, becomes somewhat irregularly direct at the later astogenetic stages. A few species do appear to be regularly directly budded ; these are *Batopora ernii* as figured by Dartevelle (1948) and *Lacrimula visakhensis*. *Batopora murrayi* also has strong tendencies to directly budded series of zooids. The very regularly directed budded zooids figured by Reuss (1867), in *Batopora rosula* are not in fact of this type (see p. 351).

If the first circle of buds is regarded as consisting of frontally budded zooids from an ancestrular complex (see below), the apparent reversal of normal zooid orientation is explicable. Theoretical explanations of reversal of the operculum and viscera, or of the proportions and roles of the basal, lateral and distal walls (see Harmer, 1957), are not necessary. In other, unrelated genera colonies do exist in which instead of a frontal wall development at the expense of other walls, the frontal wall is very restricted, and the lateral and distal walls greatly increased in extent, as postulated by Harmer (1957) for *Conescharellina*. It is interesting that these colonies have a conical shape, and may have a mode of life similar to that of the frontally budded colonies described here. For example, the lunulitiform genera *Anoteropora* and *Actisecos* are associated with ecological conditions similar to those in which the orbituliporiform and conescharelliniform genera are found.

Conescharelliniform colonies belonging to the Conescharellinidae and Orbituliporidae may be considered to have a primary zone of astogenetic change which never develops into one of astogenetic repetition (see Boardman *et al.*, 1969), because the zooids become progressively larger throughout the budding series. In some forms, such as *Atactoporidra* and some species of *Lacrimula* and *Batopora*, the primary zone may develop almost concurrently with, or be replaced by, a secondary zone of change. This secondary zone comprises a secondary series of buds which are produced from the exposed frontal walls of zooids of the first zone of change (see Fig. 3). In *Atactoporidra*, further series of such frontal buds may eventually form a primary zone of astogenetic repetition.

In the genera studied here, interpretation of colony structure, and even recognition of species, is complicated by the development of secondary and occasionally tertiary zones of change. These may involve part of the colony or the whole colony, and are accompanied by astogenetic and ontogenetic changes in the apical region.

During the course of this work we have been fortunate in having been able to examine several populations which show almost complete astogenetic series. This has not only enabled us to postulate a model for the earliest astogenetic stages, but has made it possible to infer parallel series of changes in less representative or less well-preserved populations.

Secondary, frontally budded zones of change are present in some species of all three genera principally studied. The secondary zone originates adapically in *Lacrimula* and *Batopora multiradiata*, and follows a regular, but entirely different pattern in the two genera. In *Lacrimula* (see Fig. 3B) each apical zooid produces one, or occasionally two, frontal buds directly from its exposed frontal wall. Further secondary zone buds arise in a similar fashion and in a regular sequence in an antapical direction. The adapical zooids frequently have closed orifices at the stage when the secondary buds are produced, but in more antapically placed zooids of the

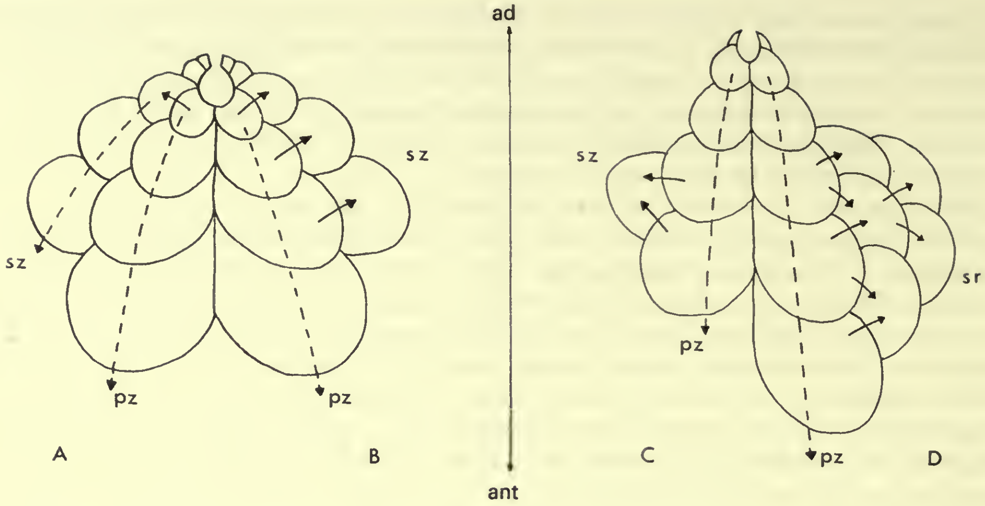


Fig. 3. Patterns of secondary budding in conescharelliniform colonies with 'frontal' astogeny. *pz,* primary zone of astogenetic change ; *sz,* secondary zone of astogenetic change ; *sr,* secondary zone of astogenetic repetition. *ad,* adapical direction ; *ant,* antapical direction.

A. Primary zone followed by antapically directed overgrowth of frontally budded secondary zone of change (e.g. *Batopora multiradiata*). B. Primary zone followed by a secondary zone of directly frontally budded zooids. Sequence of budding antapically directed (e.g. *Lacrimula*). C. Primary zone followed by isolated interzooidally budded secondary zooids (e.g. *B. clithridiata*). D. Primary zone followed by directly or interzooidally budded secondary zooids eventually forming a zone of repetition. Secondary buds often arising antapically, and sequence of budding adapically directed (e.g. *Atactoporidra*).

primary zone, the orifices are not closed by calcification, and may be seen through the orifice of the secondary frontal bud. In *B. multiradiata* (see Fig. 3A) the secondary zone arises in the same manner as in *Lacrimula,* as a circle of apical frontal buds. These zooids then proceed to bud the next generation antapically from their concealed frontal walls. This secondary zone advances, often very regularly, over the primary zone zooids. It is thus an overgrowth, but one which consists of frontally budded zooids, not those of 'normal' astogeny.

In all other species of *Batopora* secondary zooids may be produced randomly and irregularly between primary zooids as interzooidal frontal buds (see Fig. 3C). In *Atactoporidra,* the secondary zone arises antapically, in contrast to *Lacrimula,* and may extend adapically. Zooids arise as interzooidal frontal buds and in some colonies this process is continued through three generations of zooids and results in a zone of repetition (see Fig. 3D).

The astogeny of *Conescharellina* is basically of a similar pattern but differs in that the axial part of the proliferal region is filled with kenozooids, and sometimes avicularia, budded between zooids from the axial part of the concealed frontal walls. As the colony increases in size, avicularia and kenozooids arise between zooids along the whole length of the concealed frontal wall. When colony growth ceases (at various astogenetic stages which may be correlated both specifically and with unknown environmental conditions) the entire antapical area becomes covered by kenozooids and avicularia. These form a secondary zone of astogenetic change and eventually of repetition, but secondary zones of autozooids do not seem to occur in *Conescharellina*. A form of growth somewhat analogous to that of *Atactoporidra* is found in some 'celleporiform' colonies which grow on hydroids. Here the primary zone of change is formed of a small number of zooids encrusting a very restricted substratum. The major part of the colony consists of zooids of a secondary zone of change and repetition formed by frontally budded erect interzooidal zooids.

In orbituliporiform colonies a primary zone of astogenetic repetition is usually established after a variable number of generations. The zooids do not continue to increase in size, but intercalary frontally budded series are produced in both laminae.

Conescharelliform and lunulitiform genera have somewhat similar shapes and it is interesting to compare the role played by zooidal size in colony structure. In lunulitiform colonies, especially those belonging to the Cupuladriidae, which have a triadic ancestrular complex, the conical shape is achieved by the budding of intercalary rows. After the zone of repetition is established, there is little or no increase in zooid size. Even in *Cupuladria doma*, where the highly conical colony resembles that of *Conescharellina*, and where there is a small but continuous increase in size, a colony which begins with a zooidal triplet will have 30 closed peripheral zooids when it reaches full size (see Cook, 1965, fig. 3). In conescharelliniform colonies, relatively few intercalary series of zooids are produced, the conical shape resulting from a steady increase in size of the zooids of successive whorls. There are, of course, exceptions to this rule (see p. 366).

ORIENTATION OF THE COLONY, ROOTLETS AND EARLY ASTOGENY

The colonies considered here all have structures which have been observed, or may be inferred to have been associated with cuticular rootlets, which served as organs of attachment.

Orientation in life of conical and bilaminar colonies with rootlets has been the subject of a great deal of speculation in the past (see Silén, 1947; Harmer, 1957 : 724–725). It is possible that some colonies may live suspended by rootlets from algal fronds, or from hydroids, worm tubes or other Bryozoa. It is equally possible that they may be supported at or above the surface of a soft and unstable sea-bottom by rootlets which function as an anchor. These alternative theories of mode of life are not mutually exclusive, and the rootlets could perform either function.

Until observations are made upon living colonies, and their larval life and settlement preferences are known, discussion of orientation and mode of life must remain purely speculative.

Generally, those rootlets which have been observed have very thin cuticular walls, and may therefore not be comparable in function with those found in the Scrupocellariidae and Petraliellidae, which are strong enough to support the colonies above a substratum. Numbers of thin-walled rootlets would, however, have sufficient strength to support the smaller orbituliporiform colonies. Colonies of *Flabellopora* and *Lanceopora*, which are flattened and sagittate, and may be more than 30 mm in height or diameter, are known to have numerous rootlets which originate in the ancestrular region, and which are associated with kenozooids and extrazooidal tissue. From evidence of adherent Foraminifera and sand grains, these colonies are inferred to be anchored by their rootlets at the surface of the soft and unstable sea-bottoms with which they are associated. Many of the stations which have yielded specimens of these genera have also provided numerous specimens of *Conescharellina* (see Canu & Bassler, 1929a ; Silén, 1947 ; Harmer, 1957).

Rootlets have been seen in Recent specimens of *Conescharellina* and the closely related genus *Trochosodon*. These arise, principally, in the apical region, from specialized rootlet pores ('lunoecia'), which are apparently modified kenozooids budded frontally among the autozooids (see Pl. 1, figs 4 and 5), and which themselves may bud frontal avicularia (see Harmer, 1957 : 742). Not all forms of *Conescharellina* have distinct rootlet pores, however, but have complexes of kenozooids in the apical region which may form a solid structure, surrounded by avicularia, as in *C. africana* (see Cook, 1966), or a distinct tube, as in colonies of an unnamed species from Zanzibar (see Appendix 3, p. 372). These apical structures are very similar to those found in *Lacrimula* and some colonies of *Batopora*. The apical region in *Batopora* has usually been described as a 'pit'. In many colonies, a round cavity with thick calcified walls is present, surrounded by a circlet of zooids or kenozooids. In other colonies the cavity is surrounded by a raised series of kenozooids forming an external, often elongated tube. The sequence of astogenetic and ontogenetic changes is not fully known, and may be environmentally influenced, as different forms of apical structure occur among colonies of similar astogenetic age in a single population. In *Batopora* and *Lacrimula*, subsequent ontogenetic changes include a thickening of the calcified walls, and astogenetic changes consist of a proliferation of frontally budded kenozooids, presumably by adapically directed growth of units from the exposed frontal walls of the primary kenozooid and zooids. The kenozooids each have a small uncalcified area, from which it is inferred that rootlets could originate. In *L. asymmetrica*, the primary kenozooid is itself very elongated and tubular (see Fig. 6, p. 362). It appears to enlarge and become thicker walled during colony development, but whether this is an ontogenetic change, an astogenetic change or a change involving extrazooidal colony-wide calcification is not known (see Pl. 5, fig. 4). Small uncalcified areas are present upon both the external and internal surfaces of the tube. In some colonies of *B. rosula*, and in *B. scrobiculata*, the tube is apparently formed by a secondarily-budded kenozooid, which has similar uncalcified areas on its outer walls. In other species of *Lacrimula*, and in *Atactoporidra bredaniana*, the tube is composed of small kenozooids, which arise adapically as a regular series from the primary zooids (see Pl. 5). This also occurs in some colonies of *B. multiradiata*. Other changes in the apical region, found particularly in *Lacrimula*, include progressive, antapically directed closure of the orifices of the primary and later-budded zooids. At the same time, the exposed frontal walls of these apical zooids become thickened, perhaps extrazooidally. Evidence of some developmental sequences has been seen in very young colonies.

In *B. stoliczkai*, *B. murrayi*, *L. asymmetrica* and *Trochosodon* sp. a kenozooid appears to be one of a primary group of zooids. The walls of the kenozooid are calcified, but there is always a large, round, uncalcified area adapically. It is inferred that this marks the position of origin of an uncalcified rooting or anchoring element.

In *L. asymmetrica* the primary complex consists of five zooids and a long, tubular kenozooid (see Fig. 6). One of the five zooids is asymmetrical and may have been developed before the remaining four. If the kenozooid was involved in the growth of a rootlet, it was present from the earliest stage, and remained prominent, becoming larger in subsequent growth stages of the colony (see p. 362). In *B. murrayi* there is a primary pair of zooids, followed by a triad. The exposed frontal walls of the primary pair and two of the subsequent triad surround a large rounded apical cavity which itself has calcified walls. This is inferred to mark the site of an immersed primary kenozooid. In *B. stoliczkai* (see Pl. 1, fig. 1) there is a primary zooid pair and a large kenozooid with a prominent round aperture. Later stages show a 'pit' surrounded by calcification or kenozooids at this point, and it is inferred that the kenozooid is part of the primary group. A young colony of *Trochosodon* sp., a genus known to have rootlets, shows a zooidal triad and a large rounded cavity which is inferred to mark the position of a primary kenozooid. Although this colony comprises only ten zooids, it has secondarily budded apical avicularia and three semilunar rootlet pores. The general similarity of the modes of growth of these colonies is shown in Fig. 6 and on Pl. 1, figs 1–6.

Harmer (1957 : 748, fig. 78) made some interesting observations on the early development of *Trochosodon*. He remarked : 'There is doubtless some variation in the details of the early development.' He concluded that in some specimens of *T. optatus* there was an ancestrula and paired primary zooids. In view of its prominence, it is possible that the 'ancestrula' was an apical kenozooid. The specimen of *T. linearis* figured by Harmer (1957, fig. 75) was drawn from the 'basal' side by transmitted light. In reflected light from the adapical side it shows a large central cavity, with calcified walls, filled with darkly stained tissue, unlike that of the surrounding zooids. It is surrounded by one pair of very small zooids on one side, and a pair of slightly larger zooids on the other side. It is possible that the central cavity represents a primary rootlet element arising from a kenozooid.

The presence of rootlet pores in the early astogenetic stages of *Trochosodon* suggests that the analogous series of apical structures and the primary kenozooid in species without rootlet pores fulfil a similar function, especially as the colonies inhabit similar environments (see also p. 346).

The ancestrular area of conescharelliniform colonies is considered apical in the geometric sense. In the bilaminar orbituliporiform colonies the theoretical colony cone may be regarded as bilaterally compressed, with a consequent distortion of the apical region to one side of the colony. Development of kenozooidal and/or extrazooidal tissue complicates the structure of the apical region in both groups.

The exact nature of the ancestrula is not known, and as the calcified parts of the colony are not attached to, nor incorporate a recognizable substratum (as, for example, in the Cupuladriidae, which incorporate a small sand grain or foraminiferan), the earliest astogenetic changes may only be inferred. It is probable that a single

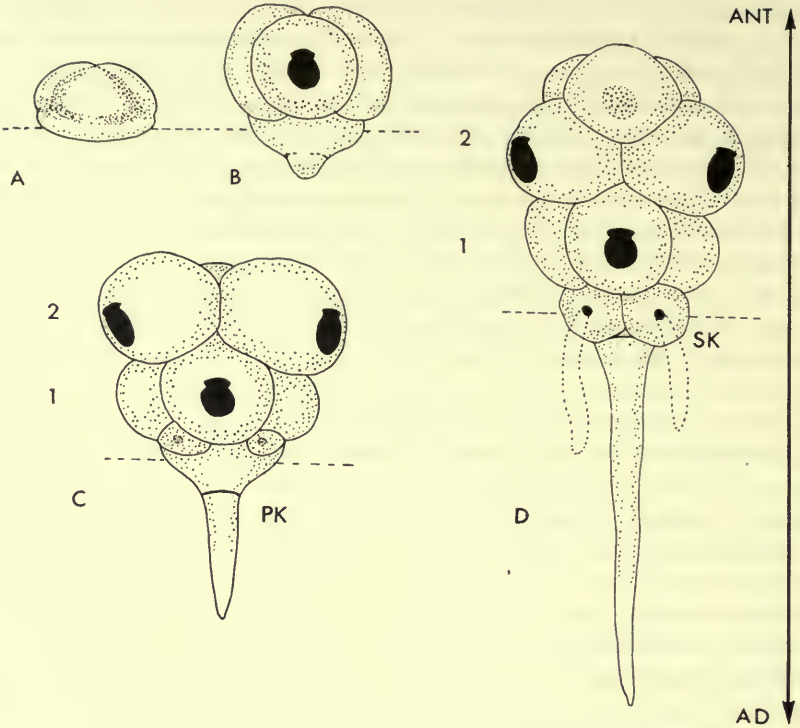


FIG. 4. Hypothetical early astogeny of a conescharelliniform colony, assuming that the apical tube produces rootlets anchored in a soft substratum. The orientation in life is unknown, but this form of astogeny would be applicable if the colonies were suspended by rootlets. AD, adapical direction ; ANT, antapical direction ; PK, primary kenozooidal rootlet ; SK, secondary kenozooidal rootlet ; 1, first zooid whorl ; 2, second zooid whorl.
A. Metamorphosed larva producing an ancestrular complex comprising one kenozooid and three zooid elements. B. First whorl of zooids complete, kenozooidal tube developing and forming primary rootlet. C. Second whorl of zooids complete, apical kenozooids forming round apical kenozooidal tube. D. Third whorl of zooids developing, apical tube now comprising several secondary kenozooids with secondary rootlets.

ancestrula with calcified walls is not developed at metamorphosis. Instead the primary whorl of zooids or kenozooids may be simultaneously differentiated within an uncalcified ancestrular complex which also includes a rootlet element. Development of such a kenozooidal rootlet or rootlets would rapidly separate the budding locus from the substratum, into which the rootlet system would become attached or anchored. Later development of apical kenozooids could also provide further rootlets, while the primary zooid whorl budded successive generations of zooids frontally in the opposite direction (see Fig. 4). This would account theoretically both for the inferred method of life, and for the absence of a substratum attached to a single, calcified ancestrula. Ancestrular complexes of 2–4 zooids are known (see Eitan, 1972, and Cook, 1973). Rootlet development may be very rapid. For example, living colonies of *Hippopetraliella africana* from Ghana have been seen to develop basal rootlets 5 mm long in 48 hours. Opposing directions of growth from an ancestrular focus were described by Harmer (1957 : 794–795) for colonies of *Adeona* with complex systems of kenozooidal rootlets. Bryozoan colonies may also be established by kenozooids, feeding zooids not appearing until later astogenetic stages, as in *Scruparia*. Thus the necessary elements for the hypothetical astogeny given in Fig. 4 do occur in Bryozoa, although they have not all been directly observed in such a combination.

A demonstration by Dr G. Eitan, exhibited in September 1974 at the 3rd International Conference of the International Bryozoology Association (Department of Geology, Université Claude-Bernard, Lyon), showed that the early astogeny of *Margaretta*, an erect jointed form, was very similar to that postulated for conescharelliniform colonies. The ancestrular complex included kenozooidal rootlets, and was adhesive, but not adherent to the substratum.

Lagaaij (1963b : 203–207), discussing the possible mode of life of *Fedora*, postulated anchoring rootlets arising from 'special chambers' associated with the zooids. One such chamber was observed with a fine, cuticular rootlet intact. He also described colonies which had incorporated fine grains of substratum material. One colony of *Batopora clithridiata* (see p. 351) from the Eocene (Hampstead, London Clay, BM 69554 pt.) shows a similar growth form. At some point in its astogeny the colony has incorporated a small sand grain, 0·60 mm in diameter. The apical zooids surround part of the sand grain, but are very irregular in shape and may belong to a secondary zone of change. The remaining zooids are budded frontally in regular alternating series.

COMPARISON OF ASTOGENETIC SERIES

Astogenetic series within a single population are rare, but it has been possible to trace the astogeny almost completely in *Lacrimula asymmetrica* (see p. 361) and partially in *L. grunaui*. Comparison of the number of zooids per whorl with the number of whorls and the total number of zooids in a colony has shown that there are some fundamental differences among species which are related to their astogeny.

For example, if there is little increase in the number of zooids per whorl throughout astogeny in the primary zones of change, the number of zooids in a colony should increase arithmetically. Differences between estimated and actual totals should be attributable to other observable astogenetic changes. This hypothesis was tested in samples which contained several colonies at different astogenetic stages (see Table 1).

In *Batopora murrayi* the number of zooids falls below that estimated because avicularia and kenozooids actually take the place of entire zooids in series. In *B. stoliczkai* the primary triad comprises one kenozooid and two zooids, and in both *B. stoliczkai* and *B. clithridiata* the actual number increases rapidly above the estimated figure as scattered, secondary frontally budded zooids occur with greater frequency. The same reason for increase occurs in one *B. rosula* colony from Crete. The larger colonies from Baden appear to have only four zooids per whorl in the

TABLE I

Comparison of astogenetic series

	No. of zooids per whorl	No. of whorls	Estimated no. of zooids	Total observed no. of zooids
Batopora murrayi	5	3	15	15
	5	4	20	18
	5	5	25	20
B. stoliczkai (first whorl has two zooids only)	3	3	8	8
	3	4	11	15
	3	5	14	18
	3	6	17	22
	3	7	20	30
B. clithridiata	4	3	12	13
	4	4	16	18
	4	5	20	28
	4	6	24	33
B. rosula (Crete)	5	4	20	21
	5	8	40	38
B. rosula (Baden)	4	4	16	17
	5	4	20	21
	7	4	28	30
	7	7	49	48
B. multiradiata	7	6	42	43
	7	7	49	49
	7	9	63	66
	7	12	84	80
	4	6	24	56
	4	8	32	60
	4	11	44	66
Lacrimula asymmetrica	5	1	5	5
	4	2	9	9
	5	3	14	14
	4	4	18	18
	5	5	23	23
	4	6	27	27
L. grunaui	4	5	20	20
	4	6	24	24
	4	9	36	36
L. perfecta	5	6	30	30
	6	6	36	36
	6	8 (estimated)	48	46
	9	11 ,,	99	86
	9	20 ,,	180	160

first whorl, but there does seem to be a production of intercalary series of zooids in the primary zone of change, which accounts for the larger totals at the same astogenetic stage as the remaining colonies from Crete. The actual numbers may fall below the estimated numbers because the production of intercalary series is not absolutely regular. Young stages of *B. multiradiata* resemble some of the larger colonies of *B. rosula* from Baden in number of zooids, which is very close to the estimated figure. They may be distinguished from nearly all other specimens of *Batopora* by the number of zooids per whorl. The colony and zooid size is, however, small. Young colonies with six to seven zooid whorls comprise 43–49 zooids; a colony of *B. scrobiculata* of comparable size (about 1 mm high and 2 mm wide) has only 24 zooids, and one of *B. murrayi* only 15. The colonies of *B. grandis* differ completely in their very large number of zooids yet apparently low number of zooids per whorl.

In *L. burrowsi* and *L. perfecta*, the proliferal region, comprising relatively few zooids of the primary zone of change, merges with a secondary zone of change, including intercalary rows, and contains a larger number of zooids.

In *L. perfecta* the apical region is rapidly covered by a proliferation of kenozooids, and the number of whorls in this region has been estimated by comparison with younger colonies. The actual number of zooids is less than that estimated, as the number of zooids in the primary whorl is unknown in large colonies, but due to the introduction of intercalary rows, is less than that in the proliferal region, on which the estimate for the whole colony is based.

In *L. asymmetrica* the number of zooids per whorl regularly alternates between four and five, because one zooid is always developed slightly earlier than the others in alternate whorls. The number does not increase arithmetically, but the agreement between the estimated and actual numbers in these colonies and those of *L. grunaui* is a measure of the regularity of growth and the absence of any secondary zooids at these astogenetic stages.

CODING OF CHARACTERS AND RESULTS OF POLYTHETIC CLUSTERING

The advantages of studying morphological relationships of bryozoan populations by polythetic clustering have recently been discussed by Cheetham (1968) and by Boardman *et al.* (1969). Apart from supplying a visual display of degrees of morphological similarity it may reveal new aspects of problems which have been hidden by previously accepted taxonomic concepts. In addition, the discipline of producing a coding for comparison of characters means that the basic nature of the 'characters' themselves is re-examined and that the specimens are subjected to a consistent series of observations and analysis (see Boardman *et al.*, 1959, fig. 1).

After analysis and clustering, under ideal conditions, the morphological relationships displayed can be tested for systematic relevance by plotting the clusters in a time-space context (see Boardman *et al.*, 1969, figs 11 and 12).

During work on the conescharelliniform species described here, we became aware of a number of exceptions to the generally accepted character-correlations within the populations studied. This was particularly noticeable when specimens were being assigned to nominal genera using the classical concepts of such groups. Great variation within samples of what appeared to be 'species' was also found, although to some extent this could be attributed to astogenetic and ontogenetic differences.

Some characters are listed in Table 2, and their occurrence compared among species assigned to the genera illustrates how arbitrary some of our decisions have been.

TABLE 2

Occurrence of characters among species.

	Conescharellina	*Batopora*	*Lacrimula*	*Atactoporidra*
1. External apical tube	1 species	*B. rosula* *B. multiradiata* *B. grandis*	all species	*A. bredaniana*
2. Colony-wide secondary zones of zooids	absent	*B. multiradiata*	*L. asymmetrica* *L. similis*	all species
3. Rootlet pores (lunoecia)	nearly all species	absent	absent	absent
4. Axial kenozooids	nearly all species	*B. rosula* *B. scrobiculata* *B. asterizans*	*L. perfecta* *L. visakhensis* *L. similis*	absent
5. Avicularia	all species	*B. murrayi* *B. clithridiata*	nearly all species	*A. bredaniana*
6. Condyles	all species	absent	nearly all species	?
7. Sinus	all species	*B. grandis*	*L. asymmetrica* *L. grunaui* *L. similis*	absent
8. Ovicells laterally displaced	*C. catella*	*B. grandis*	not displaced	not displaced
9. Ovicells apical	*C. africana*	not apical	*L. visakhensis*	not apical

In order to test concepts of both 'species' and 'genera', characters were chosen, analysed and used to assess similarity among the specimens examined. One of the most useful results of this analysis has been the demonstration of factors which must be considered both when deciding character states and when interpreting the clusters.

The biology of living specimens of conescharelliniform species is virtually unknown, and the characters used here, both quantitative and qualitative, represent only a small part of those potentially available in Bryozoa. Much finer examination of plentiful colonies may reveal, for example, characters associated with calcification of walls, intercommunication of zooids, and detailed structure of orifices, avicularia and ovicells. Further information may come from investigation of the astogenetic and ontogenetic changes occurring in the apical region.

We are here dealing with Bryozoa in which both the sample and colony size are often very small. The interaction of genetic relationships and environmental influences has apparently evolved great similarity in colony structure and zooid form among samples. Conversely, astogenetic and ontogenetic changes produce large morphological differences within samples. For example, one possibility arising from comparison of colonies at different astogenetic stages, or where relative astogenetic ages cannot be inferred, is that clusters may reflect age similarities more than 'taxonomic' similarities.

Comparison of characters of similar astogenetic age is difficult, as a zone of repetition is not usually present. Although both absolute and relative rates of astogenetic and ontogenetic change are unknown, one approximate guideline available is the comparison of colonies with the same, or nearly the same, number of zooid whorls. Because colonies rarely bud in regularly alternating or direct patterns (see p. 324), it is not always easy to decide how many zooid generations are present, and because the numbers of whorls is often low, errors are correspondingly significant. Much of the material examined is fossil, and differences among and within samples may therefore be partly the result of differential conservation. Characters and character states used are given in Table 3, and a list of the specimens in Table 4 (see also Appendices 1–3). The following notes explain some of the concepts used in defining the characters, and why difficulties were sometimes encountered in deciding which of the character states was present.

Characters 1 *and* 2. The axial length and proliferal region width of a colony not only give a measure of absolute size, but describe its shape. In conjunction with the number of zooid whorls it also gives a secondary measure of zooid size range and arrangement.

Characters 3, 4, 14, 27 *and* 28. The type, number, position and nature of astogenetic zones. All colonies comprise at least one zone of change. Coding the presence of secondary zones was confined for these characters to those consisting of zooids only. The kenozooids, interzooidal avicularia and apical structure are considered separately, as it is not known exactly when and in what sequence these may be secondary in occurrence. The numbers of whorls of zooids is counted as the number of series which it is inferred were budded simultaneously, whether alternately or directly. The number of zooids in each whorl can be inferred from the proliferal region, and in many colonies is the same or very few more than the number in the primary whorl.

Character 5. Number of zooids at the surface. Here only forms with one zone of change are strictly comparable, but the presence of very large numbers of zooids is often directly correlated with the presence of a secondary zone of change or zone of repetition.

Characters 6, 7, 10 *and* 11. The maximum length and width of exposed frontal wall. This is the equivalent of the 'classical' zooid length and width usually measured for cheilostomes. Where possible, the measurement of the third whorl zooids was taken as this gives one of the few estimates of size among colonies at a comparable astogenetic stage. The size of the subproliferal zooids is correlated with the number of whorls and the size and astogenetic age of the colony, and gives an estimate of the

TABLE 3

Characters and character states

Character	As measured or counted	State 0	State 1	State 2	State 3
1. Axial length of colony (AxL)	,,				
2. Width of proliferal region (Prl)	,,				
3. Number of whorls of zooids	,,				
4. Number of zooids/whorl	,,				
5. Number of zooids at colony surface	,,				
6. Length of exposed frontal wall of zooid of third whorl	,,				
7. Width of same	,,				
8. Length of orifice of same	,,				
9. Width of orifice of same	,,				
10. Length of exposed frontal wall of zooid of subproliferal whorl	,,				
11. Width of same	,,				
12. Length of orifice of same	,,				
13. Width of orifice of same	,,				
14. Number of zones of astogenetic change (excluding kenozooids)			one zone of change	more than one zone of change	plus zone of repetition
15. Nature of apical region		'pit' obscured by kenozooids	'pit'	external tube	secondarily budded kenozooid

16. Length of apical tube or kenozooid	,,				
17. Width of apical aperture	,,				
18. Inflation of exposed wall of subproliferal zooid			flat	slightly inflated	distinctly inflated and prominent
19. Calcification of same			smooth, tubercles <5 μ	finely granular, 5–20 μ	coarsely granular, >20 μ
20. Condyles in orifice		absent or not seen	present		
21. Sinus in orifice		absent or not seen	wider than half width of orifice	narrower than half width of orifice	
22. Position of kenozooids or closed zooids		absent	apical only	apical and/or scattered	as 2 + axial
23. Avicularia		absent	interzooidal	adventitious	
24. Ovicells		absent	present		
25. Length of subproliferal ovicell	,,				
26. Width of subproliferal ovicell	,,				
27. Position of origin of secondary zone zooids		absent	adapical	scattered	antapical
28. Nature of secondary zone zooids		absent	frontally budded	overgrowth	

TABLE 4

List of specimens analysed
(see also Fig. 5)

Number	Asto-genetic group	Name	Reference	Locality	Age
1	A	*Batopora multiradiata*	K 48–50	Spain	Oligocene
2	B	,, ,,	USNM 71205	Italy	Eocene
3	B	,, ,,	USNM 88881	,,	,,
4	A	,, ,,	USNM 71205	,,	,,
5–6	B	,, ,,	USNM 88881	,,	,,
7	D	*Batopora scrobiculata*	USNM 88882	Bavaria	,,
8	B	*Batopora grandis*	,, ,,	,,	,,
9–10	C	,, ,,	,, ,,	,,	,,
11	B	,, ,,	,, ,,	,,	,,
12	B	,, ,,	BM D31117	,,	,,
13	A	*Batopora multiradiata*	USNM 71205	Italy	,,
14 & 16	A	*Atactoporidra bredaniana*	BM D7864	Belgium	,,
15	B	,, ,,	,, ,,	,,	,,
17–18	A	*Lacrimula burrowsi*	BM 1965.8.24.11	Zanzibar	Recent
19	B	,, ,,	BM Stn 103	,,	,,
20–21	A	,, ,,	,, ,,	,,	,,
22	C	*Lacrimula pyriformis*	BM 1965.8.24.13	,,	,,
23	B	,, ,,	,,	,,	,,
24	D	*Lacrimula* sp.	BM Stn 98	,,	,,
25–26	C	,, ,,	,,	,,	,,
27	B	,, ,,	BM Stn 126	,,	,,
28–30	C	*Lacrimula visakhensis*	BM 1970.8.8.1	E. India	Holocene
31 & 33	C	*Lacrimula similis*	BG 312	Indonesia	Miocene
32	B	,, ,,	,,	,,	,,
34–35	D	*Lacrimula asymmetrica*	,,	,,	,,
36–37	C	,, ,,	,,	,,	,,
38	D	*Lacrimula grunaui*	G 5671	,,	,,
39	C	,, ,,	,,	,,	,,
40	B	,, ,,	,,	,,	,,
41	D	*Lacrimula borealis*	43/3–1	North Sea	Oligocene
42	D	*Batopora* sp.	SM 55	Italy	Miocene
43	C	*Batopora rosula*	6–27	Crete	,,
44	D	,, ,,	,,	,,	,,
45	D	,, ,,	Huelva	Spain	Pliocene
46	D	,, ,,	PLR 4607	Malta	Miocene
47	C	,, ,,	R1103	Spain	,,
48–49	D	*Batopora murrayi*	BM1965.8.24.6	Zanzibar	Recent
50–52	D	,, ,,	BM Chall. 174D	Fiji	,,
53	D	*Batopora rosula*	NMV fig. 7	Austria	Miocene
54	C	,, ,,	NMV fig. 1	,,	,,
55–56	D	,, ,,	NMV	,,	,,
57	A	*Batopora multiradiata*	BM	Italy	Eocene
58	C	*Trochosodon* sp.	BM Stn 126	Zanzibar	Recent
59	D	*Batopora clithridiata*	BM B1357C	England	Eocene
60	D	,, ,,	BM D40339	,,	,,
61	C	,, ,,	BM B1357	,,	,,

TABLE 4 (*cont.*)

Number	Asto-genetic group	Name	Reference	Locality	Age
62	C	*Batopora asterizans*	K 52	Netherlands	Oligocene
63	D	,, ,,	,,	,,	,,
64	D	,, ,,	43/3–1	North Sea	,,
65	D	*Lacrimula perfecta*	BM	Italy	Eocene
66–67	C	,, ,,	,,	,,	,,
68	C	*Conescharellina africana*	BM 1949.11.10.639	Durban	Recent
69	B	,, ,,	,,	,,	,,
70–72	C	*Batopora stoliczkai*	NMV	Bünde, Germany	Oligocene
73–74	C	,, ,,	USNM	Calbe, Germany	,,
75 & 77	C	,, ,,	NMV	Bünde, Germany	,,
76	D	,, ,,	,,	,,	,,
78	C	*Batopora* sp.	,,	,,	,,
79	D	,, ,,	,,	,,	,,
80	A	*Atactoporidra glandiformis*	BM D30077	England	Eocene

rate of astogenetic change when compared with the third whorl measurements. In a few cases, both sets of measurements are identical, as only four whorls were present.

Characters 8, 9, 12 *and* 13. The size of the orifice generally increases with each whorl; the characteristics of these measurements are similar to those of the exposed frontal wall.

Characters 15, 16, 17 *and* 22. The astogeny of the apical region. This is not easily inferred and the choice of states is somewhat arbitrary. In some forms of *Batopora*, *Lacrimula* and *Atactoporidra*, distinct units of calcification, presumably kenozooids, each with a small central pore, form the apical region as an external tube. In other forms such kenozooids are absent and the tube appears to be extrazooidal in structure, or an internal tube is present, which may also be composed of either kenozooidal or extrazooidal tissue. The correlation of types of structure with astogenetic age or sample is not clear. In *Batopora*, the internal tube may be obscured by kenozooids, or replaced by a secondarily budded kenozooid which may or may not be surrounded by other small kenozooids. In some samples an astogenetic series is present which enables the sequence of appearance of the structures to be inferred, but generally there is a great deal of variation. Kenozooids and extrazooidal tissue tend to merge with closed zooids in the apical region. In *Lacrimula*, closure consists of a calcified lamina filling the zooidal orifice, often leaving a small pore or slit centrally. Small kenozooids are often found among the zooids in *Batopora*, presumably budded frontally, but whether secondary to the primary zone of zooids is not known. They may occur adapically to antapically, and in some forms appear antapically in the axial region of the proliferal zooids.

Character 18. Inflation of the frontal walls. Inflated walls are positively correlated with long, tubular peristomes in Recent forms. Fossil specimens are usually worn but the subproliferal zooids may show distinct states of inflation and sometimes elongated peristomes.

Character 19. The degree of tuberculation of the exposed frontal wall may be affected by preservation. The majority of colonies thus appear to be 'finely granular,' but some are consistently smooth and others coarsely granular.

Character 23. Avicularia are not generally common and are usually interzooidal, budded frontally among zooids in a similar manner to the kenozooids. Structures inferred to be adventitious avicularia are very rare and occur in one species only; they are associated with the edge of the peristome.

Characters 24, 25 *and* 26. All ovicells seen are hyperstomial and usually appear to have been closed by the operculum. Some are large and prominent, others small and immersed, a few are laterally displaced. The presence of ovicells may indicate astogenetic maturity, and they are often present only in the proliferal region.

Ideally, comparison should be made only among colonies from each sample which are at exactly the same astogenetic stage, but this was not possible with the material available. Eighty colonies were therefore divided into four groups of roughly comparable astogenetic age. The division was not completely arbitrary, but endeavoured to include colonies from as many samples as possible in each group (see also Table 4).

Group A comprised 11 colonies with 15–22 astogenetic generations from 7 samples. 3 of which were also represented in Group B.
(Nos 1, 4, 13, 14, 16, 17, 18, 20, 21, 57, 80.)

Group B comprised 14 colonies with 9–13 astogenetic generations from 11 samples, 3 of which were also represented in Group A, 6 in Group C and 1 in Group D.
(Nos 2, 3, 5, 6, 8, 11, 12, 15, 19, 23, 27, 32, 40, 69.)

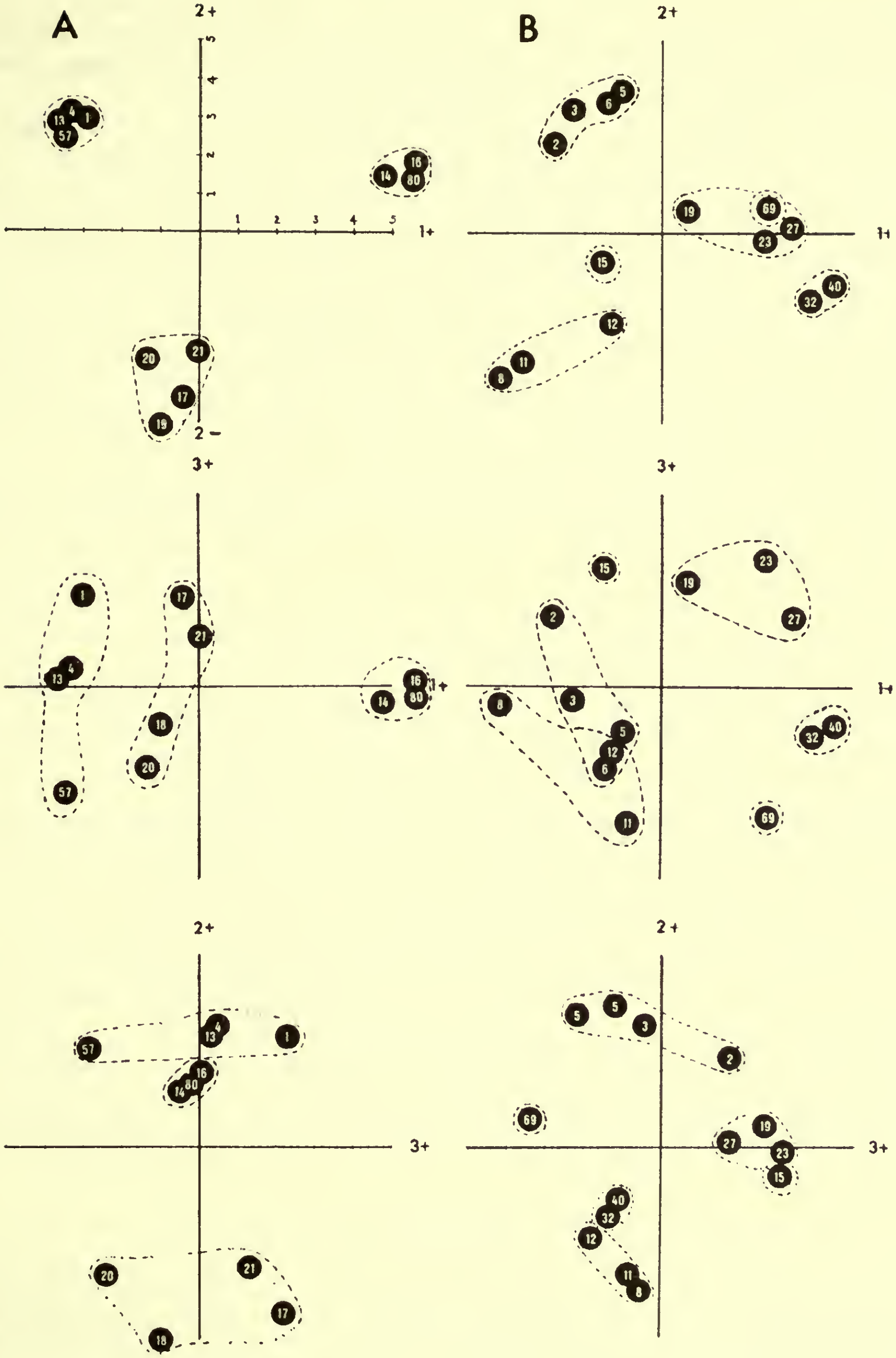
Group C comprised 31 colonies with 6–8 astogenetic generations from 18 samples, 5 of which were also represented in Group B, and 10 in Group D.
(Nos 9, 10, 22, 25, 26, 28–31, 33, 36, 37, 39, 43, 47, 54, 58, 60–62, 66, 67, 68, 70–75, 77, 78.)

Group D comprised 24 colonies with 3–5 astogenetic generations from 18 samples, 10 of which were also represented in Group C, and 1 in Group B.
(Nos 7, 24, 34, 35, 38, 41, 42, 44–46, 48–53, 55, 56, 59, 63–65, 67, 79.)

FIG. 5. Ordination diagrams, prepared by the principal co-ordinates algorithm (Gower, 1966). Squared distance in proportion to (100-similarity). See Table 4 for key to numbering; data and co-ordinates stored at BMNH.

A. Group A colonies with 15–22 zooid whorls. Co-ordinates 1 & 2, 1 & 3 and 3 & 2. Note complete separation of clusters of *B. multiradiata* (1,4,13,57), *Atactoporidra* (14,16,80) and *Lacrimula* (17,18,20,21) in three dimensions.

B. Group B colonies with 9–13 zooid whorls. Co-ordinates as above. Note degree of separation similar to that in Group A of clusters of *B. multiradiata* (2,3,5,6) *Lacrimula* (19,23,27) and *Atactoporidra* (15). *B. grandis* (8,11,12), *L. grunaui* (32,40) and *Conescharellina africana* (69) are also completely separated in three dimensions.


A
B
2+
1+
2−
3+
1
2
3
4
5
13
4
1
57
16
14
80
20
21
17
19
18
5
3
6
2
69
27
23
15
40
32
12
11
8

Results

In Group A, separation of three-dimensional clusters of the large colonies in samples of *B. multiradiata*, *L. burrowsi* and *Atactoporidra* was distinct. Within *Atactoporidra*, both species clustered together (see Fig. 5A).

In Group B, smaller colonies of *B. multiradiata*, *A. bredaniana* and *Lacrimula* maintained a similar degree of separation to that of Group A, except that within *Lacrimula*, two clusters, one of *L. burrowsi* and *L. pyriformis*, the other of *L. similis* were formed. Colonies of *B. grandis* also formed a distinct cluster (see Fig. 5B).

In Group C, a much larger number of still smaller colonies were compared, and the resulting clusters were far less distinct. *B. grandis*, *B. clithridiata* and *B. rosula* formed consistently separated clusters, but the variation within several of the other samples was apparently greater than the difference among samples of different nominal species. For example, three widely separated and variably constituted clusters of several species of *Lacrimula* were formed, and two distinct clusters of *B. stoliczkai*, one of which included *B. asterizans*.

In Group D, this within-sample diversity was maintained in *Lacrimula*. *B. rosula*, however, formed a distinct cluster, but included *L. borealis*, just as the very loose cluster of *B. murrayi* included *B. clithridiata*. *B. asterizans* again clustered with *B. stoliczkai*.

Some of this apparent confusion can be attributed to the general similarity of these very small colonies, the differences in total numbers and overall dimensions of zooids etc. being much less in groups C and D than in A and B. Ontogenetic differences such as presence or absence of ovicells also produced relatively large differences within samples which outweighed similarities in other characters. It is probable that if additional characters, and a larger number of colonies from each sample were available, the resulting clusters might be less diffuse.

Generally, the interpretation of these three-dimensional clusters has confirmed the degrees of difference among the samples reached by inspection. Until further work can be done, using a more thorough analysis of larger samples, few systematic relationships in time can be demonstrated here.

The Eocene to Oligocene samples of *B. multiradiata* may be confidently inferred to be genetically continuous, as may the Miocene to Pliocene samples of *B. rosula*. There is a very close relationship between the Oligocene *B. stoliczkai* and *B. asterizans*, and a more tenuous link may perhaps be indicated between these populations and the Eocene *B. clithridiata*. Relationships within *Lacrimula* are obviously very complex, and intermediate forms in time and space are required to establish any pattern of relationship both among the Eocene to Recent forms, and between *Lacrimula* and *Conescharellina*.

EVOLUTIONARY TRENDS IN MORPHOLOGY

Batopora, appropriately named after the blackberry, shows little evolutionary change with time. At most there is a tendency towards increasing regularity in the arrangement of the radial rows of zooids around the colony axis, but on the other hand good regularity is already present in an early, Middle Eocene (Lutetian), form like *B. scrobiculata* Koschinsky. *B. multiradiata* would seem to be an exception, with its very irregular, double-layered arrangement, and large number (120 or more) of zooids per adult colony. This irregularity is however more apparent than real (see p. 350). In most other species of *Batopora* the number of zooids fluctuates from 13 to 48 (see Table 1). There is not much of an evolutionary trend to be found in the development of either kenozooids or heterozooids. Kenozooids on the antapical surface are already mentioned in the original descriptions of the Late Eocene *B. multiradiata* and of the Oligocene *B. stoliczkai*. In the latter species other kenozooids occur among the zooids on the opposite, conical surface, just as they do in the Recent *B. murrayi*. Avicularia with a cross-bar, which occasionally occur among the zooids in the last species, are rare in the genus but also occur in one of the earliest forms, the Eocene *B. clithridiata*.

In *Lacrimula*, the principal change with time appears to be the loss of axial kenozooids, which are present in the Upper Eocene *L. perfecta* but absent in some Miocene and all Recent forms. This trend is not a simple one, however, as axial kenozooids are present in the Holocene *L. visakhensis* and the Miocene *L. similis*, but absent in the Oligocene *L. borealis*. Although one sample of *L. perfecta* contains fairly large colonies, there does also seem to have been a general increase in maximum colony size with time.

ECOLOGY AND PALAEOECOLOGY

Conescharelliniform, orbituliporiform and generally lunulitiform colonies are classically associated with calm, often deeper water, and sands, i.e. coarser-grained sediments. The evidence given below includes lithology, known and inferred depth and assemblages of Recent and fossil forms.

Nearly all Recent records of species with these three colony forms are associated with sea-bottoms of sand or mud. Lagaaij (1963a) gave details of the limits of tolerance in *Cupuladria*, and Cook (1963, 1966) has noted similar associations. The distribution of Recent *Conescharellina* is almost confined to sandy and muddy sea-bottoms (see Station data given by Canu & Bassler, 1929; Silén, 1947; Harmer, 1957). The lithology of fossil colonies shows a similar range of grain size, from calcarenite to clay (see Table 5).

Recent *Conescharellina* occurs in depths which vary from 12 m to more than 2000 m. Most records are from the range 140–450 m. Recent *Lacrimula* occurs from approximately 100 to 200 m, and *Batopora* from 285 to 805 m. Other conescharelliniform genera such as *Fedora* have been found at 2018 m (see Jullien, 1883), and *Trochosodon* occurs from 88 to 2081 m, the majority of records being from the deeper end of this range (see Harmer, 1957 : 744 for details).

Fossil records of *Batopora* carry with them the connotation of occurrence at relatively great depths. Namias (1891 : 506), for example, reported *B. rosula* from 'stradi di mare profondo' and Seguenza (1880 : 130) reported *B. rosula* as one of the commonest, and always perfectly preserved species of Bryozoa in the Tortonian clays at Benestare, Calabria, which he considered (p. 90) 'un deposito di mare considerevolmente profondo'. Le Saint (1961 : 96) referred to 'la préférence de ses formes [Batopora] pour les eaux relativement profondes'. Some occurrences of *Batopora*, however, may be inferred to be relatively shallow and neritic, two of the shallowest being (1) that of *B. rosula* with numerous *Cupuladria haidingeri*, some *C. canariensis* and some *Biflustra texturata* in the upper part of the Middle Tortonian Tefeli Formation, Almiri Section, Iraklion Province, Crete; Sissingh (1972 : 33) referred to these beds as 'deposited in a marine environment of shallow to moderately deep water'; (2) that of *B. multiradiata* in the Lower Oligocene calcarenites of Moli de Llinares, north of Villajoyosa, Alicante Province, Spain. The associated rich and diversified larger Foraminifera assemblage was listed by Cosijn (1938 : 13) and guarantees non-bathyal depth, although MacGillivray (1971 : 236) remarked, 'the formations have characteristics of gravitational deposits', i.e. may have been secondarily displaced into deeper waters. The deepest bathyal occurrences which may be inferred, on the other hand, are found in (1) the Torre Veglio Section, northern Italy, in a wash residue consisting almost entirely of planktonic Foraminifera (Schüttenhelm, pers. comm.); (2) the INI–Coparex Huelva–1 well, at 648 m below surface, in the Cadiz Basin, Spain, associated with a flood of planktonic Foraminifera and with common *Liebusella soldanii*.

TABLE 5

Correlation of sediment type, depth and assemblage of conescharelliniform colonies

Name	Reference	Age	Type of sediment	Type of assemblage	Depth (known or inferred)
Batopora clithridiata	Gregory, 1893	Early Eocene	C	O : S	
B. stoliczkai	Labracherie, 1961	Early to Middle Eocene	? AS	(M) : S	
Atactoporidra globosa	Labracherie, 1961	Early to Middle Eocene	? AS	O : S	
B. scrobiculata	Koschinsky, 1885	Middle Eocene		O : S	
A. glandiformis	Cheetham, 1966	Middle Eocene	C	O : S	55–90 m
B. multiradiata	Reuss, 1867	Late Eocene	M	O : S	
B. rosula	Malecki, 1963	Late Eocene	CS	O : S	
B. stoliczkai	Malecki, 1963	Late Eocene	CS	O : S	
Lacrimula perfecta	Accordi, 1947	Late Eocene		O : S	
A. bredaniana	Dartevelle, 1933	Late Eocene to Early Oligocene	? AS	O : S	
B. multiradiata	K 48–51, Spain	Early Oligocene	CR	O	Shallow to moderately deep
L. borealis	43/3–1, North Sea	Middle Oligocene	C	(M) : S	
B. asterizans	Boom Clay	Middle Oligocene	C	M	150–250 m (Boekschoten, 1967)
B. stoliczkai	Reuss, 1867	Late Oligocene		S	
Batopora sp.	Cheetham & Håkansson, 1972	Late Oligocene	C	O	150–200 m

TABLE 5 (*cont.*)

Name	Reference	Age	Type of sediment	Type of assemblage	Depth (known or inferred)
B. rosula	R 1103, Spain	Early Miocene	C	(M)	
B. rosula	SM 55, Italy	Early Miocene	M	M	Bathyal
B. multiradiata	Ceretti & Poluzzi, 1970	Early Miocene	CR	O	
B. rosula	MU 214, Sardinia	Early Miocene	M	M	
L. asymmetrica	BG 312	Early Miocene		S	
L. similis	BG 312	Early Miocene		S	
B. rosula	PLR 4067, Malta	Middle Miocene	C	M	
B. rosula	Reuss, 1848	Middle to Late Miocene	C	(M) : S	Bathyal (Haug, 1920 : 1637)
B. rosula	Seguenza, 1880	Middle to Late Miocene	C		
B. rosula	6–27, Crete	Late Miocene	M	M	shallow to moderately deep
B. rosula	Huelva, Spain	Pliocene	FS	M	Bathyal
L. visakhensis	Rao & Rao, 1973	Holocene	CS	O : S	89 m
B. murrayi	Cook, 1966	Recent	C	M	805 m
L. burrowsi	Cook, 1966	Recent	CS	O : S	101–207 m
L. pyriformis	Cook, 1966	Recent	CS	O : S	310 m
Conescharellina africana	Cook, 1966	Recent	Md	O : S	102 m
C. angustata	Harmer, 1957	Recent	Md	O : S	88 m
Trochosodon radiatus	Harmer, 1957	Recent	Md	M	1944 m

Sediment :

CR = Calcarenite ; C = Clay ; Md = Mud ; M = Marl ; FS = Fine-grained sand ; AS = Argillaceous sand ; CS = Coarse-grained sand.

Assemblage :

M = Monospecific ; (M) = Almost monospecific ; O = Multispecific assemblage ; S = Other specialized colony forms present in assemblage, i.e. orbituliporiform or lunulitiform colonies.

Generally, both fossil and Recent bryozoan assemblages associated with soft and unstable sea-bottoms show first an increasing number of specially adapted forms with increase in depth. This is followed by a decrease in all forms ending in monospecific occurrences at very great depths.

Harmer (1957 : 649–650) analysed the species obtained by the 'Siboga' from a few stations in the Java Sea where the sea-bottom was mud at 82–88 m ; he remarked : 'There is no group of Stations . . . in which the correlation between mode of growth and nature of the bottom is more clearly established.' Of the 39 species found, many were new, and at least 15 showed some recognizable adaptation to the specialized conditions. Eight had some form of rootlet system and six were lunulitiform species. As *Conescharellina* and *Flabellopora* are known to have rooting systems which can be associated with foraminiferal ooze, it is interesting to note the close correlation of their distributions. These two genera, often represented by several species, occur together at 20 of 36 stations listed by Canu & Bassler (1929), Silén (1947) and Harmer (1957). In addition, *Lanceopora* occurred with the above genera at eight of these stations.

Recent and Holocene records of *Lacrimula* are correlated with *Cupuladria* and *Conescharellina*. *Conescharellina* and *Trochosodon* have been found in association with as many as seven other similarly adapted species at the shallower end of their range. At great depths, both these genera tend to have monospecific occurrences, and, as noted above, one record of Recent *Batopora* is from very deep water.

Evidence from fossil assemblages gives a similar picture. Maplestone (1904 : 207, 209) gave tabulations which noted the correlation of fossil *Conescharellina* and *Lanceopora* (as *Schizoporella flabellata*, see also Maplestone, 1910). Among the specially adapted forms such as *Kionidella*, *Stichoporina* and *Lunulites*, *Orbitulipora* is one of the commonest genera found in association with specimens of *Atactoporidra* and *Batopora* (see, for example, Ossat & Neviani, 1897 ; Gregory, 1893 ; Malecki, 1963 ; Labracherie, 1961).

Batopora multiradiata is generally associated with diversified bryozoan faunas, but the three very deep records of *Batopora* mentioned above, two fossil and one Recent, are conspicuously monospecific, and it is only one step further to suggest that *all* monospecific occurrences come from the deep end of its bathymetric range. There is nothing in the data at hand (Table 5) to contradict this suggestion. The Lower and lower Middle Miocene of the Mediterranean area seem to be particularly marked by such monospecific deep-water occurrences, and in keeping with the inferred depth, the associated lithologies tend towards the finer grain-sizes ; either marl or calcareous clay (Table 5).

DISTRIBUTION IN TIME AND SPACE

Historically, the oldest published record of a conescharelliniform colony is that of *Batopora*, in Soldani's figure of '*Historices marinas minimas*' (Soldani, 1780, pl. 16, figs 83Q, R ; figures copied by Annoscia, 1968, pl. 1, figs 8a, b). According to the original plate explanation (p. 130) these fossils originate from 'the valley East of San Quirici'. Dr Annoscia kindly informs us that 'The location of the samples containing *Batopora*, according to Soldani's words, is "not far from Caitro [nowadays unknown] S. Quirico, in a place above the Fosso di Rifigliuoli [now 'Fosso Refiglioli' see map] named Poggi di Rifigliuoli (Soldani, 1780, pp. 130 e 35, art. III), 1 mile from Castello [now unknown or destroyed] beyond the Fosso di Rifigliuoli toward S. Quirico" [some 35 km S.E. of Siena]. I think it might be the circled place on the enclosed map, named today "Podere Favorito", or not far from it.'

'The formation "Upper marine clay and lower ocreaceous shale" by Soldani might belong to the formation "P_{ag}^{2-1}" in the new edition (1968) (sheet 121) of the official geological map printed by the Italian Geological Survey. This formation is made by clay, sandy clay, also in continental facies ("Piano del Sentino" Fm.) associated with small lenses or layers of puddingstone, locally with Lower–Middle Pliocene microfauna.'

Time-stratigraphically, *Batopora clithridiata* (Gregory) from the London Clay (Ypresian) of the London Basin and the forms described by Labracherie (1961, pl. 16, figs 2 and 4) as *Batopora stoliczkai* from the subsurface Lower Eocene of the Bordeaux area, France, vie for the distinction of being the oldest *Batopora* on record. From then onwards the genus occurs in all younger Tertiary stages in Europe (Table 5) with the exception of the Uppermost Miocene. Data are too few, however, to assess whether this absence is fortuitous or indeed reflects the Late Miocene (Messinian) 'Crise de salinité' in the Mediterranean (Hsu, Ryan & Cita, 1972). For more than a century *Batopora* has been considered an extinct genus, until recently one of us found a living representative in the western Indian Ocean, near Zanzibar (Cook, 1966). It appears that *Batopora* had disappeared from western Europe after the Oligocene, and that most Miocene and Pliocene records are from the Mediterranean and Paratethys (Map 1, p. 369). In the Pliocene the genus had even ventured out into the western Atlantic. Its present occurrences near Zanzibar and Fiji are curiously remote from the palaeodistribution even in the not-so-distant past, although naturally this may only reflect our ignorance of deeper-water Tertiary faunas from the Indian and the Pacific Oceans.

In contrast to *Batopora*, the genus *Lacrimula* was first described by one of us (P. L. C.) from the Recent, east African coast, and was then found by the other (R. L.) in fossil assemblages from western Europe and the East Indies. Specimens from the Holocene of the northern Indian Ocean have also since been described by Rao & Rao (1973) (see Map 2, p. 370).

Atactoporidra apparently never had a wide distribution, and there are no records after the Oligocene. The three species recorded were from the English and French Eocene, and from the Belgian Eocene and Oligocene.

Conescharellina may have been present in the Eocene of western Europe, although records of species may prove to be referable to *Lacrimula* (see p. 359). The genus seems to have had an almost constant presence in the Australasian region from the late Oligocene to the Recent. (Dr R. Wass, in an unpublished report on stratigraphic ranges of some Bryozoan species from the Tertiary of south-eastern Australia (unpublished report in the Geological Sciences, University of Sydney, 1973 – derived in part from Cockbain, 1971) gives the age of the Mount Gambier fauna as late Oligocene–early Miocene.) *Conescharellina* was common during the Australian Miocene, and there are records from the Pleistocene of the East Indies and Japan. Kataoka (1957) found no *Conescharellina* in a cold-water, Pliocene fauna from Northern Honshu, Japan (approximately 40°N, 140°E). However, by Pleistocene times, probably during an interglacial period, the genus was present further south, at Kikai Jima (approximately 28°N, 130°E, see Kataoka, 1961 : 259). The accompanying large bryozoan fauna included many tropical and subtropical species, including the orbituliporiform *Flabellopora*, and the lunulitiform *Cupuladria* and *Actisecos*. Recent records extend even further north, up to 41°N, 140°E (see Canu & Bassler, 1929b) and west to East Africa (see Map 3 and Appendix 3, pp. 371–373). Generally, the distributions given here may be interpreted as wide, warm water occurrences during the Eocene and Oligocene, which have either shifted or become progressively restricted in a southerly and easterly direction up to the Recent.

CONCLUSIONS

It has become apparent during this study that the classical concepts both of structure and taxonomy of conescharelliniform colonies require much further work. Analysis of many more samples from additional areas and horizons may begin to throw light upon their evolutionary systematics. At present, we may reach the following conclusions and indicate some of the directions of future research which may prove fruitful.

The overall effects of genetic constitution and environmental selection outweigh microenvironmental effects in colony structure. The conescharelliniform colony has a rigid astogenetic pattern allowing for little variation in the primary zone of change, but allows more in secondary zones, especially in the apical region. Here environmental influences may be the reason for the latitude in astogenetic and ontogenetic expression both within and among populations.

It is possible that convergent lines of evolution with parallel development have occurred, and this possibility requires further investigation.

The obvious physical separation and finiteness of colonies make them very susceptible to statistical analysis of samples. Comparative astogenetic age of colonies within samples is essential. The within-population variation of species requires analysis in the hope of following environmental changes in population characteristics.

Integration within colonies is considerable. A low degree of integration is expressed in colonies where zooids have little interdependence and function in a manner similar to that of solitary animals. Boardman & Cheetham (1973 : 132–134) have suggested several characters with sequences of states showing increasing integration among bryozoan colonies. Using these sequences the wall structure, interzooidal communication, astogenetic zonation and polymorphism of conescharelliniform colonies illustrate a high degree of integration. The devolution of roles among zooids and kenozooids at the earliest astogenetic stages, and the continued development of patterned polymorphs and extrazooidal tissues, are particular examples of colony-wide control.

The specialized mode of life allows palaeoecological inferences to be made as to the depth and nature of the sea-bottom through a considerable range of time.

Future studies on larger samples of more populations should include further examination of type or topotype material of described species. A systematic search of fine-grained sediments, both fossil and Recent, should be made, to enlarge knowledge of distribution and abundance in time and space. Eventually, this should include parallel studies on other orbituliporiform and conescharelliniform species both with 'normal' and 'frontal' astogeny.

A study of similar colony forms such as that exhibited by *Sphaeropora*, which has a Tertiary to Recent range, may throw some light on the evolution of the colony form (see also Waters, 1919 : 80).

The possibility of a study of living colonies may be remote but should not be neglected. The breeding and above all the settlement and early astogeny of a single species would provide guidelines applicable with confidence to other forms.

DESCRIPTIONS OF SPECIES

Family **ORBITULIPORIDAE**

Orbituliporidae Canu & Bassler, 1923 : 186.

Ascophora with discoidal and bilaminar, or conical colonies, which may be multilaminar. Zooidal calcified frontal wall extensive, cryptocystidean, consisting of two elements, one of which contributes to the exposed surface of the colony and which surrounds a centrally placed orifice. Orifice oval, frequently with paired condyles, occasionally with a distinct antapical sinus. Ovicells usually large, hyperstomial, directed adapically, occasionally immersed. There is constantly a tube, comprising kenozooids and/or extrazooidal tissue, which in some cases extends beyond the colony surface, and which is in contact with the ancestrula or ancestrular complex internally. It is inferred that the tube marks the origin of rootlets which anchored the colony to its substratum. The tube is radially placed in bilaminar (orbituliporiform) colonies, and axially placed in conical (conescharelliniform) colonies. Avicularia and kenozooids often present.

Genus ***BATOPORA***

Batopora Reuss, 1867 : 233. Type species *B. stoliczkai* Reuss.

Reuss formally introduced *Batopora* as a new genus, when describing *B. stoliczkai*. Other species were referred to the genus in the discussion, but were not formally described. They included *Cellepora rosula*, which Reuss had described in 1848, and *Conescharellina angustata* d'Orbigny. Waters (1919 : 93) formally listed *B. stoliczkai* as type species of *Batopora*. Canu & Bassler (1917 : 75), however, had already listed '*Batopora rosula* Reuss 1847' as the type species of the genus, which they quoted erroneously as '*Batopora*, Reuss 1847'. This was emended in later works, and Canu & Bassler (1920 : 629) and Bassler (1935 : 54 ; 1953 : G230) gave the type species as *B. stoliczkai*.

Some previous attributions of species to *Batopora* need examination of specimens before they can be assigned to the genus with any confidence. Among these *B. aviculata* Héjjas (1894 : 214, 251, pl. 6, fig. 11) is problematical, and *Batoporella eocaenica* Héjjas (1894 : 215, 252, pl. 7, fig. 13) seems to be related to *Orbitulipora*. Both forms were reported with records of '*B. conica* Hantken' (see p. 359), *B. multiradiata*, *B. rosula* and *B. scrobiculata* from the Eocene of Hungary.

Colony conescharelliniform, with an external or internal adapical tube. Zooids with antapical edge of orifice flattened, peristomes frequently raised, tubular and prominent, exposed frontal walls of zooids often inflated, especially in the proliferal region. Avicularia sometimes present, mandibles hinged on a bar. Ovicells large, hyperstomial but often immersed and obscured by the peristome. Secondary zones of change formed by frontal budding. Secondary series of zooids forming overgrowths in some species.

The species previously described in this genus fall into two groups; those in which there are a large number of zooids (maximum seen 200) in a colony, and in which frontal budding of secondary overgrowth is found, and those with a smaller number of zooids (rarely more than 50), in which secondary zooids are irregular in occurrence and in which overgrowth does not occur.

The apical region may be marked by an internal kenozooidal or extrazooidal tube (the 'pit' of authors) or by an external tube. In some colonies the tube appears to be replaced by a secondarily budded kenozooid.

The first group is represented by *B. multiradiata* and *B. grandis*. In *B. multiradiata* the colonies often reach a considerable size (3 mm in diameter), and are marked by the development of a distinct type of secondary zone of astogenetic change. Secondary zooids arise adapically, and apparently form an overgrowth of zooids advancing over the primary zone in a regular manner. Each zooid is budded frontally from the concealed part of the frontal wall or walls of zooids of the new proliferal region (see p. 326). This secondary zone is a modified form of overgrowth and thus differs radically both from 'normal astogeny' overgrowth and from frontal budding (see Banta, 1972). It also differs from the type of secondary zones of change found in *Atactoporidra* and *Lacrimula* (see p. 326).

The secondary zone of change does not always develop regularly, especially during its later astogeny. Few populations of *B. multiradiata* are well preserved, and wear increases their irregular appearance. We have been able to examine two well-preserved populations, which show the astogeny both of the primary and secondary zones of change particularly clearly.

Specimens from the Val di Lonte and Montecchio Maggiore (Eocene, Bartonian, Italy, USNM 71205, 7 colonies and 71196, 4 colonies) average 1·25 mm in axial length and 2·75 mm in proliferal region width. Nearly all these colonies possess a distinct raised apical tube apparently composed of extrazooidal tissue, and surrounded by a circlet of kenozooids. The secondary astogenetic zone of zooids can be seen to arise in two colonies as a circlet of eight very small zooids just below the tube. The primary zone consisted of regularly alternating whorls of six zooids. The number in the proliferal zone of secondary zooids varies from 30 to 40 (see Pl. 3, fig. 1; Pl. 4, figs 5–6).

Ovicells are present throughout the primary zone and in the last 1–4 whorls of the secondary zone. They are large, very prominent, and have a regularly pitted surface, which may indicate the presence of pseudopores in life. Orifices of brooding zooids are wide, with a distinct antapical peristome. Other colonies from Götzreuth (USNM 88881, Eocene, 65 colonies) may not all belong to *B. multiradiata* but several show clearly that the secondary zone consists of zooids budded frontally in alternating series as an overgrowth of the primary zone (see Pl. 4, fig. 4). Here, too, ovicells are present in both primary and secondary zones. These specimens include some very young colonies (see Table 1).

B. grandis also possesses large colonies with numerous zooids. It may produce intercalary rows of zooids, but does not develop a distinct secondary zone of overgrowth.

The second group includes all other known species of *Batopora.* The colonies are never very large, and secondary zones of change are limited to isolated zooids budded frontally from exposed frontal walls of primary zone zooids. This group may be subdivided into species with globular colonies with small zooids (*B. stoliczkai*, *B. clithridiata* and *B. asterizans*) and those with a more conical shape and larger zooids (*B. scrobiculata, B. rosula* and *B. murrayi*).

Specimens of *B. stoliczkai* from the Lower Oligocene of Saale (see p. 352), have small colonies with very small zooids and frequently occurring interzooidal kenozooids. Avicularia are absent, but the ovicells are very well preserved and quite prominent. Isolated secondary zooids are fairly frequent in the larger, astogenetically older colonies (see Pl. 1, fig. 1 ; Pl. 2, fig. 2 ; Pl. 3, fig. 4).

B. clithridiata was described as *Conescharellina clithridiata* by Gregory (1893 : 252, pl. 31, figs 10 and 11), from specimens from the London Clay at Sydenham (South London) and Hampstead (North London). The figured colony was separated from a large number from Sydenham (BM 1357) which remained in the Collection under a manuscript name. Nearly all the specimens possess some interzooidal avicularia with a complete bar, many also have small interzooidal kenozooids and isolated secondary zooids (see Pl. 2, fig. 1 ; Pl. 5, fig. 5). *B. clithridiata* has slightly larger zooids than *B. stoliczkai*, in other characters they are very similar.

B. rosula was first described by Reuss (1848 : 78, pl. 9, fig. 17) as *Cellepora rosula*, from the Miocene of Baden, Austria. These specimens have not been examined, but those he described later (1867 : 225, pl. 1, figs 7a–c ; pl. 2, figs 1a–c) have been seen. Reuss apparently illustrated two distinct astogenetic stages of *B. rosula.* Both possess a small, external apical tube, apparently composed of kenozooids, and in both the zooid series were figured as budding directly. The two figured specimens differ in their alternate budding pattern from Reuss's drawings. The remaining three specimens in Reuss's material show a fairly high range of variation. Two of them are irregular in development, and one has a secondarily budded conical kenozooid apically instead of the complex kenozooidal tube of the other colonies. The calcification of the zooids varies from medium to coarsely granular. Generally all five colonies are well preserved and most have ovicells. These are not prominent, and the frontal surface has a distinctly punctate appearance. Axial kenozooids are present in some colonies, and the apical region shows either a small aperture (presumably a pit) surrounded by slightly raised kenozooids or a narrow, raised tube with rows of radially arranged pores on its surface. This tube greatly resembles a zooid in size and shape and seems to be a product of later astogenetic changes in the colony. One colony is worn adapically, and shows traces of the walls of the ancestrular region in section. The primary zooid tetrad surrounds a circular area which presumably marks the position of the apical kenozooid or kenozooidal tube (cf. *B. stoliczkai*, p. 352, and see Pl. 3, figs 2 and 3).

The other Miocene specimens from the Mediterranean area assigned here to *B. rosula* are well within the range of variation shown by Reuss's specimens. The colonies from Malta and Crete (see Pl. 4, figs 1 and 2) are slightly smaller, and have a secondary kenozooid apically. One specimen from Spain (Roep 1103), which has ovicells, is almost exactly like the colony figured by Reuss (1867, pl. 1, fig. 7).

B. scrobiculata was described by Koschinsky (1885 : 63, pl. 6, figs 2a–c, 3a–c) from the Eocene of Götzreuth. A specimen from this locality (USNM 88882 pt), labelled *B. scrobiculata*, has a flatter colony shape than *B. rosula*, the zooids are very large, comparable with those of *B. grandis* and *B. murrayi*, and easily distinguishable from those of *B. rosula* at a similar astogenetic age. The calcification of the zooids is coarsely granular and axial kenozooids are present (see Pl. 3, figs 5, 6 and 7). The Pliocene *Batopora* from Huelva, Spain, has somewhat similar characters. It has a flattened colony, and the calcification of the large zooids is coarsely granular. In view of its age and locality, it should, however, perhaps be assigned to *B. rosula*.

Batopora stoliczkai Reuss

(Pl. 1, fig. 1 ; Pl. 2, fig. 2 ; Pl. 3, fig. 4)

Batopora stoliczkai Reuss, 1867 : 223, pl. 2, figs 2–4.

MATERIAL EXAMINED. Lower Oligocene, Bünde, Germany, 27 colonies, NMV, 1867.XII, 13a–d. Lower Oligocene, Calbe, Saale, Germany, 5 colonies, USNM.

DESCRIPTION. Colony small, globular. Maximum number of whorls 7. Maximum number of primary zooids in proliferal whorl 3. Maximum number of primary buds 2.

AxL	0·63–0·90 mm	Prl	0·87–1·06 mm
Lfw	0·21–0·23 mm	lfw	0·23–0·25 mm
Lo	0·09–0·10 mm	lo	0·08–0·09 mm
Lov	0·16–0·17 mm	lov	0·18–0·23 mm

REMARKS. The five colonies from Calbe have almost the same characteristics as those from Bünde, except that interzooidal kenozooids are more frequently and regularly developed. The kenozooids do not appear to have any uncalcified central portion, and the small zooid-like structures figured by Reuss (1867, pl. 2, figs 2a, b) as occurring between zooids are thus not exactly as depicted. Among the small kenozooids, the partially closed, half-submerged orifices of primary zone zooids are often visible, below the surface of the secondary zone interzooidal zooids. The antapical axial kenozooids are exactly as figured by Reuss (pl. 2, fig. 3). Of the 32 colonies examined, seven of the specimens from Bünde differ in several ways from the majority. Three colonies are worn, regularly oval in shape and larger than all the others. They appear to have been composed of alternating series, and more than one zone of zooids. The largest colony measures 1·40 mm in axial length and 0·90 mm in proliferal width and comprises approximately 49 zooids. It is very probable that these three colonies are late astogenetic stages of *B. stoliczkai*. Two of the remaining colonies are probably attributable to *Batopora*, but differ from *B. stoliczkai*. They consist of 22 and 30 zooids respectively, arranged in rather irregular whorls of 5–6 zooids each. The colonies are flatter than those of *B.*

stoliczkai (AxL, 0·52–0·64 ; Prl, 1·12–1·30) and have a wide, internal apical tube, surrounded by kenozooids. There are no antapical kenozooids. It is possible that they are representatives of yet another form of *Batopora*, but further specimens would be required to ascertain their specific position.

The two remaining colonies resemble *B. stoliczkai* in zooidal characters, but appear to be at least partially bilaminar. The focus of budding is at the periphery of each colony, from which point alternating zooids are produced facing in opposite directions. These form an astogenetic gradient, becoming larger and more regularly bilaminar so that the colonies form rounded wedges. It is possible that these colonies are very young astogenetic stages of *Orbitulipora*.

Although these last four colonies differ widely from the others, it is just possible that they are variants of *B. stoliczkai* induced by unknown environmental factors, and much more analysis of larger populations would be needed before any further conclusions as to their relationships could be made.

One colony from Bünde shows a very early stage in the astogeny, which may be compared with those described for *Lacrimula asymmetrica* (p. 361). The primary, almost certainly ancestrular, complex consists of a triad of two zooids and a kenozooid. The zooids have elongated peristomes, the kenozooid a wide rounded orifice hardly raised above the remainder of its exposed frontal wall. Two further whorls are present, each consisting of alternating triads of zooids (see Pl. 1, fig. 1). The antapical surface at this stage is flat, and consists of the concealed frontal walls of the last triad only, no kenozooids are present. The next stage present (from Calbe) has 15 zooids and only four whorls of zooids. The four zooids in excess of the estimated number (see p. 333) are secondarily budded zooids arising between those of the first and second whorls. In all larger colonies, secondary buds are more regularly triadic than those in *B. clithridiata*, and tend to be produced in sequence, about one astogenetic generation behind the zooids of the primary zone. The presence of a narrower proliferal region produces the globular appearance of the colonies, which also have a more regular aspect than those of *B. clithridiata* after the 12–14 zooid colony stage, as the small kenozooids are budded between the zooids.

The similarity among young stages of *B. stoliczkai*, *B. murrayi*, and *Trochosodon* sp. is illustrated on Plate 1, figs 1–6.

Batopora grandis[1] sp. nov.

(Pl. 2, figs 5, 6 ; Pl. 3, fig. 8)

HOLOTYPE. Eocene, Götzreuth, Bavaria, BM D31117.

OTHER MATERIAL EXAMINED. Lutecian, Eocene, Götzreuth, Bavaria, with *B. scrobiculata*, *B. multiradiata* and *K. excelsa*, 4 colonies, USNM 88882 ; paratypes.

DESCRIPTION. Colony large, elongated, conical. Maximum number of whorls 12. Maximum number of zooids in proliferal whorl 4. Maximum number of primary buds unknown, probably 4.

---

[1] *grandis* – (L) – large – referring to the large size of the zooids.

AxL	1·88–2·72 mm	Prl	1·70–2·00 mm
Lfw	0·40–0·45 mm	lfw	0·35–0·60 mm
Lo	0·14–0·20 mm	lo	0·10–0·12 mm
Lov	0·32–0·50 mm	lov	0·35–0·55 mm

Apical region an internal tube surrounded by small kenozooids. Zooids very large, arranged in directly budded series with secondary zooid series apparently budded regularly between them, forming a spiral pattern. Exposed frontal walls of zooids not inflated, finely granular. Approximately 12 marginal pores in each exposed frontal wall and 8 in each concealed frontal wall. Orifices not raised, apparently with an antapical sinus. Avicularia absent. Ovicells very large, asymmetrically displaced laterally.

REMARKS. The colonies are elongated and very large, and form an astogenetic series. The zooids are very wide and have a spiral arrangement. It is not known whether the orifices are primary or secondary, and most are worn, but some show a distinct and elongated antapical sinus. The apical region consists of a very narrow tube surrounded by 2–3 series of small kenozooids or secondary closed zooids. The number of zooids is very high, especially as there are only four (occasionally an asymmetrically-arranged fifth zooid is present) in the proliferal region. This strongly suggests that the intercalary series of zooids found on the colony surface are budded as in *Lacrimula burrowsi*, which also has a very regular appearance. There is no observable second layer of zooids in the subproliferal region of either of these species, in contrast to *L. similis* and *B. multiradiata*, where the limits of the secondary zone are strikingly obvious.

The ovicells are broken in all specimens and occur on proliferal region zooids only. They are very large, with thick, apparently two-layered walls. Each ovicell is asymmetrical and they resemble those described by Harmer (1957 : 733) in *Conescharellina catella*.

The characters of *B. grandis* are distinct from all other species, but it has features in common with *Lacrimula*, *Atactoporidra* and *Conescharellina*. In size and shape and the possession of an apical tube it resembles *L. burrowsi* and *Atactoporidra bredaniana*. The apparently sinuate orifice and asymmetrical ovicells are superficially, at least, similar to those found in some Recent forms of *Conescharellina*.

B. grandis does not appear to have been described before. It is part of a very interesting fauna of conescharelliniform and similar colonies, all from the Götzreuth locality, which includes *Kionidella*, *B. multiradiata* and *B. scrobiculata*.

Batopora asterizans[1] sp. nov.

(Pl. 2, figs 3 and 4)

HOLOTYPE. Middle Oligocene, 45°95·3′N, 1°31·6′E, North Sea 43/3–1 well, 960–990 ft, BM D52567.

OTHER MATERIAL EXAMINED. As above, 840–870 ft, 3 colonies ; 870–900 ft, 5 colonies ; 1110–1140 ft, 1 colony ; 1530–1560 ft, 1 colony ; paratypes. Rupelian, probably Middle Oligocene, Ijzendijke, Zeeland, boring K62, Boom Clay, 5 colonies; paratypes.

---

[1] *aster* – (L) – a star – referring to the stellate appearance of the apical and axial kenozooids.

Description. Colony small, conical to globular. Maximum number of whorls 6. Maximum number of zooids in proliferal whorl 3. Maximum number of primary buds 3.

AxL	0·70–0·75 mm	Prl	0·90–1·00 mm
Lfw	0·20–0·25 mm	lfw	0·25 mm
Lo	0·06–0·09 mm	lo	0·07–0·09 mm

Apical region apparently consisting of a secondarily budded kenozooid. Zooids arranged in alternating series, with small globular kenozooids arising interzooidally and usually alternating with the zooids. Circles of apical kenozooids and a group of axial, antapical kenozooids present. Frontal walls of zooids distinctly, almost coarsely granular. Exposed frontal walls inflated, with six marginal pores. Primary orifices not seen, secondary orifices oval. Ovicells and avicularia not seen.

The apical region is marked by an inner circle of five, and an outer circle of eight, alternating, globular kenozooids (diameter 0·14 mm). These presumably have overgrown the primary zooids, and also occur, budded interzooidally, fairly regularly in alternating series among the zooids. A further, axial group of five kenozooids is also present.

Remarks. *B. asterizans* has a similar growth form to that of *B. stoliczkai* and *B. clithridiata*. The arrangement of the zooids and alternating kenozooids is, however, much more regular than in either of these species. It further differs from *B. clithridiata* in the absence of avicularia.

The colonies are all very small and none have ovicells. It is therefore possible that larger colonies may eventually be found, although ovicells occur in both *B. stoliczkai* and *Trochosodon* (see Pl. 1, figs 5 and 6; Pl. 2, fig. 2) in colonies of comparable size to those of *B. asterizans*. Generally the colonies are regularly constructed, although one from the North Sea shows several frontally budded secondary interzooidal zooids which results in an appearance very similar to that of *B. clithridiata*.

The apical tube is raised and appears to consist of a secondarily budded kenozooid. It is regularly surrounded by small, rounded kenozooids, which are inferred to be secondarily budded, as one very small colony from the North Sea shows only three kenozooids, whereas larger examples show two series of 5–8 kenozooids.

Genus *LACRIMULA*

Lacrimula Cook, 1966 : 217. Type species *L. burrowsi* Cook.

Colony conescharelliniform, with an external tube. Zooids with rounded orifices, and often well-developed paired condyles, sinus occasionally present. Interzooidal avicularia sometimes present. Ovicells large, hyperstomial, prominent. Secondary zone of frontal buds arising directly from exposed frontal walls of primary zone zooids, beginning adapically.

Specimens ascribed here to *Lacrimula* vary from small elongated colonies which have some morphological affinity to the *Batopora rosula* group (*L. borealis*) to complex colonies with well-developed zones of secondary zooids which approach, superficially at least, those of *Atactoporidra bredaniana* and *Batopora multiradiata*.

Some species also show an interesting similarity in character with *Conescharellina*. Both *L. visakhensis* and *L. perfecta* possess regular axial series of kenozooids, and *L. visakhensis* resembles *C. africana* in producing adapical ovicells.

Generally *Lacrimula* includes species in which the colony is elongated and the apical region consists of a prominent kenozooidal tube.

Lacrimula burrowsi Cook

(Pl. 5, figs 1, 6; Pl. 6, fig. 3; Pl. 8, figs 1–6)

Lacrimula burrowsi Cook, 1966: 218, pl. 2, figs 2–4; fig. 4A.

MATERIAL EXAMINED. Recent, Zanzibar, 101 m, 207 m, 37 colonies, BM John Murray Coll. 1965.8.24.7–10, 1965.8.24.11; paratypes. Off Umvoti River, S. Africa, 102 m, 34 colonies, BM Burrows Coll., 1949.11.10.642.

DESCRIPTION. Colony elongated, often slightly flattened in one direction. Maximum number of whorls 19. Maximum number of zooids in proliferal whorl 6. Maximum number of primary buds 6.

AxL	2·00–3·20 mm	Prl	1·24–1·88 mm
Lfw	0·30–0·37 mm	lfw	0·30–0·45 mm
Lo	0·10–0·15 mm	lo	0·10–0·11 mm
Lov	0·14–0·30 mm	lov	0·15–0·17 mm

Apical region a tube with closely spaced external pores. Zooids primarily budded in alternating series, with avicularia frequently, but often irregularly interspersed. Frontal wall of zooids finely granular. Exposed part of frontal wall with 4–6 marginal pores, 4–6 pores in concealed part. Primary orifice divided at the mid-line by large condyles. Ovicells large, occurring in the proliferal and subproliferal zone zooids. Fertile orifices not dimorphic, closed by the operculum. Avicularia arising as frontal buds between adjacent primary zooids. Chamber large, but not reaching the axial region of the colony. Exposed part of frontal wall of chamber with marginal pores. Semicircular mandible hinged to large, paired condyles. Rostra directed adapically and slightly laterally, sometimes alternating in radial series.

The first whorl of individuals below the apical region consists of avicularia; these are secondary in origin. Secondary calcification affects zooids progressively from the apical region in an antapical direction. In some colonies the first seven whorls are comprised of zooids with closed orifices, which may have a small central rounded opening.

REMARKS. A large number of colonies of *Lacrimula burrowsi* have recently been found in bottom sediment samples kept by the Mineralogy Department of the British Museum (Natural History). The samples were all from the Zanzibar area and were collected by the John Murray Expedition to the Indian Ocean. The colonies were dried and were therefore restored in trisodium phosphate solution and stained before being mounted in epoxy-resin and sectioned. These sections have shown details which generally support some of the inferences about colony structure suggested here.

The marginal pores appear in longitudinal section as small tubules, often filled with stained tissue, passing through the thick calcification of the concealed frontal wall of one zooid into the living chamber of the next successive zooid. Tubules tend to be concentrated towards the axial end of zooids (see Pl. 8, figs 1 and 2). They are very similar in appearance to the extended 'areolar' tubules, which are derived from frontal septulae, in other Bryozoa.

The apical region shows the ancestrular whorl of zooids to be surrounded by very thick calcification. A series of large tubular pores, each surrounded by calcification, forms the apical tube (see Pl. 8, fig. 5). The pores are inferred to be the coelomic cavities of kenozooids ; they are often filled with stained tissue and pass from the exterior of the apical tube into a large interior cavity. This cavity is lined with stained tissue and it is inferred from analogy with the marginal pore tubules that neither the axial kenozooid nor the smaller kenozooids forming the tube had any connection directly with the exterior environment in life, but may have been the site of rootlets. Although elongated tubules extend from the primary zooids to the secondarily budded avicularian chambers at the base of the kenozooidal tube, there does not appear to be any communication among the small kenozooids. If the axial cavity marks the position of the coelomic cavity of a kenozooid, the smaller cavities would have been able to intercommunicate. Generally, all these structures need much more work, in this and other species, particularly those which can be demonstrated to have rootlets. The apical structures in *L. burrowsi*, however, appear to be consistent with the postulate that they were the site of rootlets arising from highly modified kenozooids which were budded successively in an adapical direction from a large axial kenozooid.

Lacrimula visakhensis Rao & Rao

(Pl. 6, fig. 4)

Lacrimula visakhensis Rao & Rao, 1973 : 506, fig. 1.

MATERIAL EXAMINED. Holocene, Bay of Bengal, E. India, 89 m, 4 colonies, BM Subba Rao Coll. 1970.8.8.1 A–D.

DESCRIPTION. Colony small, conical. Maximum number of whorls 7. Maximum number of zooids in proliferal whorl 8. Maximum number of primary buds 8.

AxL	1·12–2·20 mm	Prl	1·60–2·00 mm
Lfw	0·23–0·25 mm	lfw	0·25–0·40 mm
Lo	0·12–0·18 mm	lo	0·10–0·16 mm
Lov	0·25–0·32 mm	lov	0·30–0·40 mm

Apical region a tube with large external pores. Primary zooids budded in direct series. Secondarily budded series of zooids confined to the adapical end of the zoarium. Axial region composed of small kenozooids. Frontal wall of zooids very finely granular. Marginal pores 2–6 in exposed part of frontal wall, 8–11 in concealed part. Primary orifice oval, divided adapically to the mid-line by small, paired condyles. Both adapical and antapical parts curved; peristome absent. Ovicells very large and wide, orifice wider than long. Brooding zooids budded secondarily from zooids at the adapical end of the colony. Frontal surface of ovicell granular, marginal pores present. Avicularia arising as frontal buds between adjacent zooids in the adapical region; mandibles inferred to have been rounded. Avicularia are not common, occurring laterally beside a zooidal orifice in a few zooids only; they have no bar or condyles and are inferred to be avicularia only by their size and position.

The first whorl of zooids in the young colony is hidden by a whorl of avicularia which are budded between the primary zooids.

REMARKS. The condyles of the autozooidal orifices are placed distinctly adapically, those of brooding zooids are not visible. The ovicells occur in a single whorl at the adapical end of the colony, and all arise as secondary zooid buds between primary zooids.

Antapically the concealed frontal walls of the youngest proliferal region zooids show that the marginal pores do not extend axially to the limit of each zooid. They form a row half-way across the wall. The axial region is filled with 6–8 very small kenozooids.

L. visakhensis differs from other species of *Lacrimula* in the position of the condyles, and in the astogeny, position and frontal wall characteristics of the ovicells. It resembles *L. perfecta* in possessing axial kenozooids, and *Conescharellina africana* in the apical position of the ovicells.

Lacrimula perfecta (Accordi)

(FIG. 7A; Pl. 4, fig. 3; Pl. 7, fig. 1)

Conescharellina perfecta Accordi, 1947 : 105, figs 1–7; Braga & Munari, 1972.

MATERIAL EXAMINED. Priabonian, Upper Eocene, Cunial Quarry, Possagno, N. Italy, 16 colonies and several fragments, collected by Drs E. Annoscia and P. Ascoli, 1968. Priabonian, Upper Eocene, Forte di San Leonardo, Verona, N. Italy, 31 colonies, collected by Dr G. Braga.

DESCRIPTION. Colony conical to pyriform. Maximum number of whorls 20. Maximum number of zooids in proliferal whorl 9. Maximum number of primary buds 6.

AxL	0·75–3·40 mm	Prl	0·86–2·80 mm
Lfw	0·19–0·40 mm	lfw	0·20–0·45 mm
Lo	0·09–0·12 mm	lo	0·09–0·14 mm
Lov	0·17–0·20 mm	lov	0·25–0·30 mm

Colony with a distinct kenozooidal apical tube with external and internal uncalcified pores. Tube becoming very large, bulbous and thick by accretion of kenozooids during astogeny (1·00 mm in diameter), with a very small central aperture at the apex (0·10 mm in diameter). Axial kenozooids also budded regularly in series forming a central core (1·60 mm in diameter). Zooids with a non-sinuate orifice, wider antapically, with paired lateral condyles. Zooids budded in alternating series; later, intercalary series also budded. Avicularia small, regularly budded between two orifices, oval with a complete bar, mandible directed laterally. Ovicells present in larger colonies, fairly prominent and globular.

REMARKS. The attribution of this form to *Conescharellina* in the past was dependent on the possession of regularly patterned avicularia and axial kenozooids. Both these characteristics now appear not to be exclusive to *Conescharellina*. Regularly patterned avicularia also occur in *L. grunaui* and in many colonies of *L. burrowsi*, although in both this last species and *L. perfecta* there are colonies in which the occurrence and distribution of avicularia are much less regular. Axial kenozooids are present in *L. visakhensis*, *L. similis* and *L. perfecta*. The general distinction between the two genera has thus become progressively restricted to the nature of the primary orifice and, to a lesser extent, to the nature of the apical region of the colony.

Sinuate orifices occur in *L. asymmetrica* and *L. grunaui*, but do not have the very distinct, narrow sinus usually associated with species of *Conescharellina*. All other species assigned to *Lacrimula* have rather large, non-sinuate orifices, which tend to be wider rather than narrower antapically. The apical region in *Lacrimula* is typically formed by a kenozooidal tube; that in *Conescharellina* by kenozooids, avicularia and 'lunoecia' (rootlet pores). Forms of *Conescharellina* from E. Africa (*C. africana* and an unnamed species of *Conescharellina*, see Appendix 3, p. 372), apparently have no rootlet pores. *C. africana* has an accumulation of kenozooids, ringed by avicularia, but no axial aperture (see Cook, 1966 : 215). The other species of *Conescharellina* has a small but distinct kenozooidal tube apically.

The correlation of apical region with orifice shape, although not exclusive, has decided the attribution of *C. perfecta* to *Lacrimula*.

Accordi (1947 : 108, figs 8–10) also described another form, *C. veronensis*, from the same Italian deposits. An analysis of further samples from the area was made recently by Braga & Munari (1972), who concluded that *C. veronensis* was a synonym of *C. perfecta*.

The nature of the larger Upper Eocene specimens does, however, raise another problem. A species with a conescharelliniform colony was described as *C. eocoena* by Neviani (1895 : 122, fig.) from the Eocene of Mosciano, near Firenze. Only one specimen was found and that was not well preserved. Its principal characters were rounded orifices and, possibly, small avicularia between zooids ('piccolo aperture vibracolifere (?) sul solco superficiale che divide i vari zoeci'). The colony had an axial length of 2·33 mm, and a proliferal width of 1·47 mm. Neviani considered that *C. eocoena* was close to '*Batopora conica* Seguenza (non Hantken)' which had been described and figured earlier in very similar terms (see Seguenza, 1880 : 42, pl. 4, fig. 10). Seguenza's specimens were from the Tongrian (Oligocene) of Antonimina, Reggio Calabria. Waters (1921 : 424) regarded Neviani's, Seguenza's and Hantken's species as synonymous, but pointed out that '*B. conica* Hantken' was almost certainly a manuscript name.

The lack of well-preserved type specimens for examination, together with the nomenclatural confusion inherent in using Seguenza's name, which antedates that of the Recent form, *C. conica* Haswell (1880 : 42, pl. 3, figs 7 and 8), suggests that, for the present at least, the name used for his Eocene record should be *C. eocoena* Neviani. Specimens in the British Museum, Palaeontology Department, labelled '*Batopora conica* Hantken' from the Hantken Collection (B3724 Buda, Szaboi beds, Lower Clay, Eocene) were mentioned by Waters (1921 : 424). These colonies are very large (AxL 4·00–6·50 mm, Prl 3·50–4·00 mm) and very worn. Their appearance is, however, similar to that of the far better preserved large specimens of *L. perfecta* from San Leonardo. The orifices are rounded, and there are small pores between them placed regularly as are the avicularia in *L. perfecta*. Series of axial kenozooids are present, and the bulbous apical region (diameter 2·00 mm) has a very small central aperture. These colonies are associated with many other, mainly erect species of Bryozoa, and with *Lunulites* and *B. multiradiata*.

It thus appears possible that some, perhaps all, fossil records of *Conescharellina* from western Europe may prove to belong to one species-complex, attributable to *Lacrimula*.

Lacrimula borealis[1] sp. nov.

(Pl. 7, figs 4, 5)

Holotype. Middle Oligocene, 45°95·3′N, 1°31·6′E,. North Sea 43/3–1 well, 1430–1470 ft, BM D52568.

Other material examined. As above, 840–870 ft, 1 colony; 1860–1890 ft, 1 colony; paratypes.

Description. Colony small, conical. Maximum number of whorls 6. Maximum number of zooids in proliferal whorl 3. Maximum number of primary buds 3.

AxL	0·50–1·20 mm	Prl	0·90–1·15 mm
Lfw	0·38–0·50 mm	lfw	0·40–0·55 mm
Lo	0·16–0·22 mm	lo	0·15–0·17 mm
Lt	0·28–0·50 mm		

Apical region a long narrow, prominent tube with granular calcification and occasional pores. Zooids large, with frontal wall very slightly inflated, with 6–8 marginal pores. Peristome absent, primary orifice large, rounded adapically, straight antapically, apparently without condyles. Avicularia and ovicells not seen (see below).

Remarks. The colonies are obviously at a very early astogenetic stage, but the zooids are very large in comparison with other species of comparable age. The kenozooidal tube is long, with 4–8 regularly spaced pores on its outer surface, and a very small apical aperture.

Each of the three colonies includes one peripheral zooid which has a small, rounded foramen (approximately 0·07 mm in diameter) in the wall adapical to the orifice

---

[1] *borealis* – (L) – northern – referring to the distribution of the species.

(see Pl. 7, fig. 5). The cavity behind the foramen does not appear to be confluent with the zooid living chamber. By analogy with other species, this would therefore appear not to be a brooding zooid with adapical ovicell. The lack of other structures such as condyles, etc., also make it unlikely to be an avicularium, and as the chamber is apparently part of a zooid, it cannot be interpreted as a kenozooid. Until more specimens can be found, the nature and possible function of these distinctive structures is unknown.

Lacrimula asymmetrica[1] sp. nov.

(Fig. 6 ; Pl. 5, fig. 4 ; Pl. 7, fig. 3)

Holotype. Miocene, 07°00′S, 113°00′E, Kombangan, W. Madura, Indonesia, Tertiary f^1, *Globigerinatella insueta* zone (see van der Vlerk & Postuma, 1967, fig. 1), BG 312, BM D52569.

Other material examined. As above, 39 colonies ; paratypes.

Description. Colony pyriform, asymmetrical. Maximum number of whorls 7. Maximum number of zooids in proliferal whorl 4–5 alternating. Maximum number of primary buds 1 + 4.

AxL	0·55–1·50 mm	Prl	0·42–0·88 mm
Lfw	0·17–0·25 mm	lfw	0·15–0·25 mm
Lo	0·08–0·13 mm	lo	0·05–0·10 mm
Lt	0·15–0·30 mm		

Apical region a tube, with closely spaced, small external pores. Whorls of zooids alternate in number from 4 to 5 so that the whorls are only approximately arranged in a plane perpendicular to the colony axis, and the outline is asymmetrical. Secondary frontal buds forming a secondary zone of change are first produced at the adapical end of the colony. Frontal walls of zooids very finely granular and apparently non-porous, except for occasional marginal pores. Primary orifices of primary zooids with a very narrow adapical shelf which terminates abruptly to form paired condyles. Adapical part of the orifice sub-circular, the antapical part rounded-triangular, slightly narrower. No peristome present. Primary orifice of secondarily budded zooids ovate, apparently without condyles. Ovicells and avicularia not observed.

Remarks. Secondary calcification has affected at least two whorls below the apical region, completely closing the orifices, or leaving a semi-lunar slit. The specimens of *L. asymmetrica* comprise an almost complete astogenetic series, from the early stage of one whorl of zooids to the development of the secondary zone of astogenetic change.

The earliest stage present has only five zooids. The colony measures 0·45 mm in axial length and 0·40 mm in proliferal region width. Among these zooids there is one, which may have been slightly earlier in development than the others, slightly asymmetrical in position. The ancestrular region is completed by an apical, axial

---

[1] *asymmetros* – (G) – asymmetrical – referring to the shape of the colony.

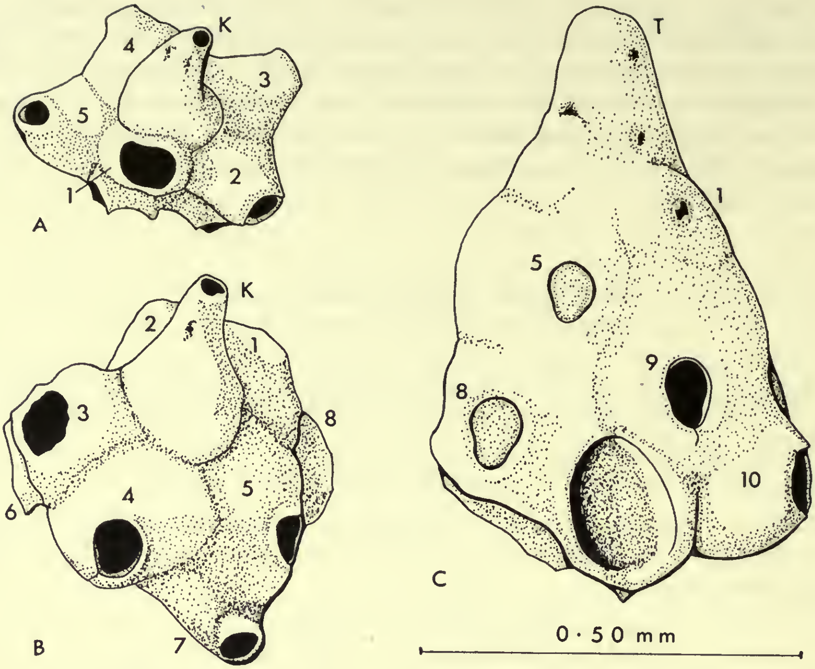


FIG. 6. Early astogenetic stages in *Lacrimula asymmetrica* sp. nov.

A. Colony comprising apical kenozooid and first whorl of 5 zooids (1 is asymmetrically developed). This colony has slightly smaller zooids than those of others at the same stage. K, kenozooid.

B. Colony comprising apical kenozooid, first whorl of 5 and second whorl of 4 zooids. K, kenozooid.

C. Colony comprising apical kenozooidal tube, enlarged by astogenetic development of kenozooids, or by ontogenetic thickening of primary tube, or by extrazooidal tissue, or a combination of any or all methods. Note three whorls of zooids present (5, 4, 5), total 14; the first whorl zooid orifices are occluded. T, apical kenozooidal tube.

elongated kenozooid, its tube extending 0·15 mm above the colony surface. Other young colonies show slight variations on this theme, but it is interesting that the alternating whorls of 4–5 zooids are present in the earliest stages, as is the kenozooidal tube, which in some cases reaches 0·20 mm in length at this stage. Later development consists of the budding of further alternating whorls and of the appearance of rugosities and pores on the surface of the kenozooidal tube, which becomes both thicker and longer. It is not known whether this is the result of kenozooidal budding, growth of extrazooidal tissues or both. By the time the colony has reached a size of 1·50 × 0·50 mm, and comprises 18 zooids, the tube may be 0·30 mm in length and may have expanded to a width of nearly 0·20 mm and be covered by 15–20 pores or depressions. The first whorl of orifices is often closed by calcification at this stage, and appears to have become incorporated into the calcification of the kenozooidal tube. At this stage, or even earlier, growth of the secondary zone begins. It starts with the production of frontal buds almost simultaneously from the second and third zooid whorls and extends, apparently fairly rapidly, to the remaining whorls. The primary zooids may also produce frontal buds, but at a slightly later stage. Some, but not all, of the primary zooids may have orifices closed by calcification when the buds are produced; in others the orifices of the primary zone zooids may be seen through the orifice of the secondary zooid.

Lacrimula grunaui[1] sp. nov.

(Fig. 7B; Pl. 7, fig. 2)

Holotype. Miocene, 07°00′S, 114°00′E, Batuputih, E. Madura, Indonesia, Tertiary f^{1}, *Globigerinatella insueta* zone (see van der Vlerk & Postuma, 1967, fig. 1), G 5671, BM D52570.

Other material examined. As above, 6 colonies; paratypes.

Description. Colony elongated, pyriform, slender. Maximum number of whorls 10. Maximum number of zooids in proliferal whorl 4. Maximum number of primary buds 4.

AxL	0·81–1·60 mm	Prl	0·70–0·88 mm
Lfw	0·20–0·25 mm	lfw	0·20–0·25 mm
Lo	0·11–0·13 mm	lo	0·07–0·10 mm
Lt	0·10–0·20 mm		

Apical region a tube, with closely spaced, small external pores. Each zooid with a consistently placed antapical avicularium. Frontal walls of zooids very finely granular, apparently non-porous, except for occasional marginal pores. Primary orifice with distinct, paired condyles, which separate a sub-circular adapical portion from a large, semicircular but narrower antapical part. No protruding peristome present, but the adapical side of the orifice is slightly raised. Ovicells not observed. Avicularian chambers situated adjacent to the central part of the concealed frontal wall, not reaching the colony axis. Exposed part of avicularian chamber very small, triangular, with a delicate cross-bar, the rostrum rounded-triangular and antapically directed.

The orifices increase rapidly in size (1·5 times in 5 whorls). Secondary calcification affects the first two whorls below the apical region. It has almost closed the orifices, leaving a vertical slit.

Remarks. *L. grunaui* differs from *L. asymmetrica* in the very symmetrical growth of the zooid whorls, and in the possession of avicularia.

Lacrimula similis[2] sp. nov.

(Fig. 7C; Pl. 6, figs 1, 2)

Holotype. Miocene, 07°00′S, 113°00′E, Kombangan, W. Madura, Indonesia, Tertiary f^{1}, *Globigerinatella insueta* zone (see van der Vlerk & Postuma, 1967, fig. 1), BG 312, BM D52571.

---

[1] Named for Dr H. R. Grunau, who collected the specimens.

[2] *similis* – (L) – resembling – referring to the similarities of this species with both *L. grunaui* and *Conescharellina*.

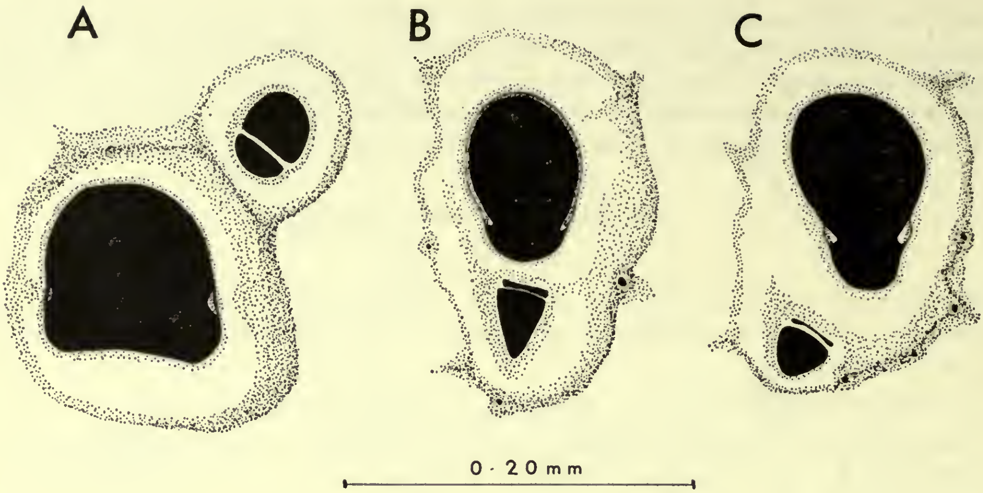


FIG. 7. Orifice and interzooidal avicularium in *Lacrimula*. A. *L. perfecta*. B. *L. grunaui*. C. *L. similis*. Scale = 0·20 mm.

OTHER MATERIAL EXAMINED. As above, 12 colonies; paratypes.

DESCRIPTION. Colony conical, irregular. Maximum number of whorls (secondary zone) 10. Maximum number of zooids in primary proliferal whorl 4. Maximum number of zooids in secondary proliferal whorl 10. Maximum number of primary buds 4.

AxL	1·16–1·36 mm	Prl	1·20–1·44 mm
Lfw	0·25–0·26 mm	lfw	0·25–0·26 mm
Lo	0·12–0·14 mm	lo	0·08–0·12 mm
Lt	0·08–0·15 mm		

Apical region originally a short tube, later surrounded by secondary and tertiary zone zooids and transformed into a shallow pit. Zooids budded in alternate series. Frontal wall smooth. Primary orifice with minute condyles, delimiting a distinct antapical sinus. Avicularia arising as frontal buds, placed asymmetrically on one side of the antapical part of the orifice which is raised as a peristome. Avicularian rostrum rounded, with a complete bar, directed laterally and antapically. Subrostral chamber large. Ovicells not seen. Small, rounded axial kenozooids formed late in astogeny.

REMARKS. The size and position of the avicularia distinguish this species from *L. grunaui*, to which it appears to be closely related. It also differs in the very early development of secondary and even tertiary zones of change, neither of which has been found in colonies of *L. grunaui* of similar size and astogenetic age. The primary zone of change apparently consists of whorls of four zooids, but as few as three to four whorls are present when the secondary zone of change appears. It begins as a series of small buds arising apically and surrounding the small, shallow kenozooidal tube. The secondary zone consists of zooids budded directly frontally from primary zooids and is not an overgrowth. Primary zone orifices may be seen through those of secondary zone zooids as in *L. asymmetrica*. The zone is very regular, a complete whorl being budded simultaneously and the sequence is in an antapical direction. Superficially, the colonies may resemble those of *B. multiradiata* as the secondary zone zooids advance on a front over those of the primary zone. In some colonies a third zone arises antapically. The avicularia are enlarged in comparison to the zooids and seem to form a special group comparable with those found in *Conescharellina africana* (see Cook, 1966). In fact, *L. similis* superficially resembles some species of *Conescharellina* with its adapical avicularia and sinuate orifices. It also develops axial antapical kenozooids which cover the concealed frontal walls of the proliferal region zooids.

Genus *ATACTOPORIDRA*

Atactoporidra Canu & Bassler, 1931 : 22 ; new name for *Atactopora* Canu & Bassler, 1929b : 50 (preoccupied). Type species *Atactopora bredaniana* (Morren).

Canu & Bassler placed this genus in the Orbituliporidae and described the colony as 'libre'. Their generic description described the zooids as 'amoncelées en désordre les unes sur les autres'. Additional information is now available as to the character of the genus, and the description has therefore been somewhat modified.

Colony conescharelliniform, with an apical kenozooidal tube. Primary zooids budded in alternating series. Secondary to quaternary series of zooids budded concurrently with the later zooids of the primary series, originating from the exposed frontal walls of the primary zone zooids, either directly or in alternating series.

Three species of *Atactoporidra* have been described, *A. bredaniana*, *A. glandiformis* and, more recently, *A. globosa* (see Labracherie, 1961). *A. glandiformis* was discussed by Cheetham (1966 : 106, fig. 81). In this species there seems to be an actual increase in the number of zooid series in the primary zone, as well as an increase in size. Similarly budded series of zooids arise antapically quite early in the astogeny, but the apical region is rarely affected.

Atactoporidra bredaniana (Morren)

(Pl. 5, fig. 2 ; Pl. 6, fig. 6)

Atactopora bredaniana (Morren) Canu & Bassler, 1929b : 51, pl. 4, figs 1–6.
Atactoporidra bredaniana (Morren) Canu & Bassler, 1931 : 22, pl. 4, figs 5 and 6 ; Dartevelle, 1933 : 85, 108.

MATERIAL EXAMINED. Eocene, Wemmel sands, Laeken, Belgium, 4 colonies, BM Dartevelle Coll., D33249–59. ? Eocene, Belgium, 20.11.1905, 50 colonies, BM Vassall Coll., D7864.

Description. Colony elongated, pyriform, irregular. Maximum number of whorls 22. Maximum number of zooids in proliferal whorl 6. Maximum number of primary buds 4.

AxL	2·20–4·60 mm	Prl	0·80–1·20 mm
Lfw	0·30–0·35 mm	lfw	0·30–0·32 mm
Lo	0·13–0·16 mm	lo	0·10–0·11 mm
Lov	0·14–0·16 mm	lov	0·15–0·17 mm
Lt	0·15–0·30 mm		

Apical region with a short tube with external pits and ridges of calcification. Frontal wall of zooids finely granular, marginal pores not seen. Primary and secondary zooidal orifices apparently without condyles. Ovicells hyperstomial, prominent, associated with tertiary and quaternary zooidal series. Avicularia not budded frontally. At the sides of the raised peristomes of some ovicelled zooids, there is a small pore, which is inferred to have been an adventitious avicularium.

Remarks. The four specimens previously examined by Cook (1966 : 217) are worn, and had developed several series of secondarily frontally budded zooids before preservation. The basic structure of the colony was therefore not readily apparent. Examination of the more plentiful, astogenetically younger, and better preserved material from the Vassal Coll. not only enables the astogeny of the colony to be inferred but shows that *Atactoporidra* and *Lacrimula* have many more characters in common than was first realized.

The specimens (D7864) include colonies in which the irregular series of secondary buds are not much developed, and in which a distinct apical kenozooidal tube is present. The arrangement of the primary zooids is regular and alternating. The orifices of the zooids are small, rounded adapically and nearly straight antapically. The ovicells have been seen in a few specimens only, and all have broken frontal walls. They are present only on the tertiary to quaternary zooidal series, are randomly placed and irregularly orientated.

The greatest concentration of secondary to quaternary frontal budding is in the antapical part of the colony, causing irregularity of outline and a confused appearance of the surface. The budding apparently occurs at the apical end of the colony at a late astogenetic stage. No progressive closure of zooidal orifices from the apical end has been seen as in *Lacrimula.* Secondary zooidal series appear to arise directly from the exposed frontal walls of primary zooids, but tertiary and quaternary series often arise alternately between zooids of the secondary series, and their orientation is irregular.

One colony of *A. bredaniana* from D7864 is rod-shaped and measures 3·00 mm long by 1·00–1·20 mm wide. The zooids of the primary zone of change are visible adapically. Secondary zooids comprise the antapical part of the colony, which is hardly wider than the adapical part. Some colonies may therefore show very little increase in size of zooids in the primary zone of change. It is not possible to see whether a primary zone of repetition occurred.

Dartevelle (1933) reported *A. bredaniana* not only from the Wemmel sands (Bartonian) but from the earlier Lédien ('gravier de base, sables à *N. variolarius*') which he equated with the Upper Bracklesham of England. Many other bryozoan species, including *Lunulites*, were present.

ACKNOWLEDGEMENTS

Permission of Shell Internationale Petroleum Maatschappij, B.V. to publish this paper is gratefully acknowledged. I should like to thank particularly Mr J. W. C. van der Sijp, Dr H. R. Eckert, Dr J. Keij and Dr R. A. Pohowsky of Shell for all their help during the final stages of preparation. Acknowledgements are also made to Rothamsted Experimental Station for use of CLASP program and computer time.

A large number of colleagues and correspondents have contributed over a period of years to the observations made here. The names of some of those who assisted us were known only to Dr Lagaaij, and I therefore apologize for any omissions. Foremost among those who have lent or presented specimens, and given advice on stratigraphical problems, etc. are: Dr E. Annoscia (Paleontologo dell'A.G.I.P., Milan), Dr G. Braga (Università di Padova), Dr A. H. Cheetham (U.S. National Museum), Dr J. J. Hermes (Geologische Institut de Universiteet, Amsterdam), Dr J. Keij (Koninklijke Shell Exploratie en Productie Laboritorium), Dr M. Subba Rao (Geology Department, Andhra University, Waltair), Dr O. Schultz (Naturhistorisches Museum, Wien), Dr N. Vavra (Paläontologisches Institut der Universität, Wien) and Prof. Dr E. Voigt (Geologisches und Paläontologisches Institut, Hamburg).

A demonstration of some aspects of conescharelliniform morphology and distribution was presented in September 1974 at the 3rd conference of the International Bryozoology Association, held at the Department of Geology, Université Claude Bernard, Villeurbanne, Lyon. Discussions with and suggestions from colleagues attending the conference are gratefully acknowledged.

I should also like to thank colleagues at the British Museum (Natural History), particularly Dr M. Hills for help and advice on statistical analysis, and Dr D. R. C. Kempe and Mr H. A. Buckley (Department of Mineralogy) and Dr B. Rosen and Mr R. Wise (Department of Palaeontology) for their help, and for access to the collections in their care.

Finally, I am deeply grateful to Mr P. J. Chimonides of the Bryozoa Section for all his help, particularly in preparation of specimens and thin-sections, and for scanning microscopy and photography.

P.L.C.

SUMMARIES IN FRENCH AND GERMAN

Les colonies conescharelliniformes et orbituliporiformes de Bryozoaires, et l'occurrence dans les deux groupes de deux formes de bourgeonnement, le 'normal' et le 'frontal', sont décrits. Les genres *Conescharellina* et *Trochosodon* sont connus d'être fixés aux leurs substrata par les petits racines. Ils sont comparés avec les genres *Batopora*, *Lacrimula* et *Atactoporidra*. On suggère un modèle hypothétique pour la croissance primaire de la colonie dans ces genres. Les caractères et le distribution dans le temps et dans l'espace de genres *Batopora*, *Lacrimula*, *Atactoporidra* et *Conescharellina* sont discutés, et on enregistre l'information à l'égard de leur écologie et leur paléoécologie. Les descriptions complètes sont donnés de trois espèces de *Batopora*, dont deux espèces sont considerées d'être nouvelles, et de sept espèces de *Lacrimula*, dont quatre espèces sont considerées d'être nouvelles. Les efforts combinés de génétique et d'environment surpassent les influences micro-environmentales dans les limites de la colonie. L'intégration dans les colonies même est considérable, elle est démontrée par les communications interzooidales, la zonation astogénétique et le polymorphisme. La manière de vivre particulière permets que les conclusions paléoécologiques soient faites quant à la profondeur et le type du fond de la mer, depuis le Eocène jusqu'au Récent.

Conescharelliniforme und orbituliporiforme Kolonien von Bryozoen und das Auftreten von zwei Typen von Astogenie, 'normaler' und 'frontaler', in beiden Gruppen werden beschrieben. Die Gattungen *Conescharellina* und *Trochosodon*, die durch Würzelchen mit ihrem Substrat verankert sind, werden mit den Gattungen *Batopora*, *Lacrimula* und *Atactoporidra* verglichen. Ein hypothetisches Modell für die Anfangsentwicklung der Kolonien dieser Gattungen wird vorgeschlagen. Die Merkmale und die zeitliche und räumliche Verbreitung der Gattungen *Batopora*, *Lacrimula*, *Atactoporidra* und *Conescharellina* werden diskutiert und die verfügbaren Daten über ihre Ökologie und Paläo-Ökologie werden angeführt. Drei Arten der Gattung *Batopora*, zwei davon neu, und sieben Arten der Gattung *Lacrimula*, vier davon neu, sind ausführlich beschrieben. Der kombinierte Einfluss von Genetik und Umwelt überwiegt die Mikroeinflüsse innerhalb der Kolonie. Integration innerhalb der Kolonien ist beträchtlich und drückt sich aus in interzooidaler Kommunikation, astogenetischer Zonenbildung und Polymorphismus. Die spezialisierte Lebensweise gestattet paläo-ökologische Schlüsse über die Tiefe und Beschaffenheit des Meeresbodens vom Eozän bis zur Jetztzeit.

APPENDICES

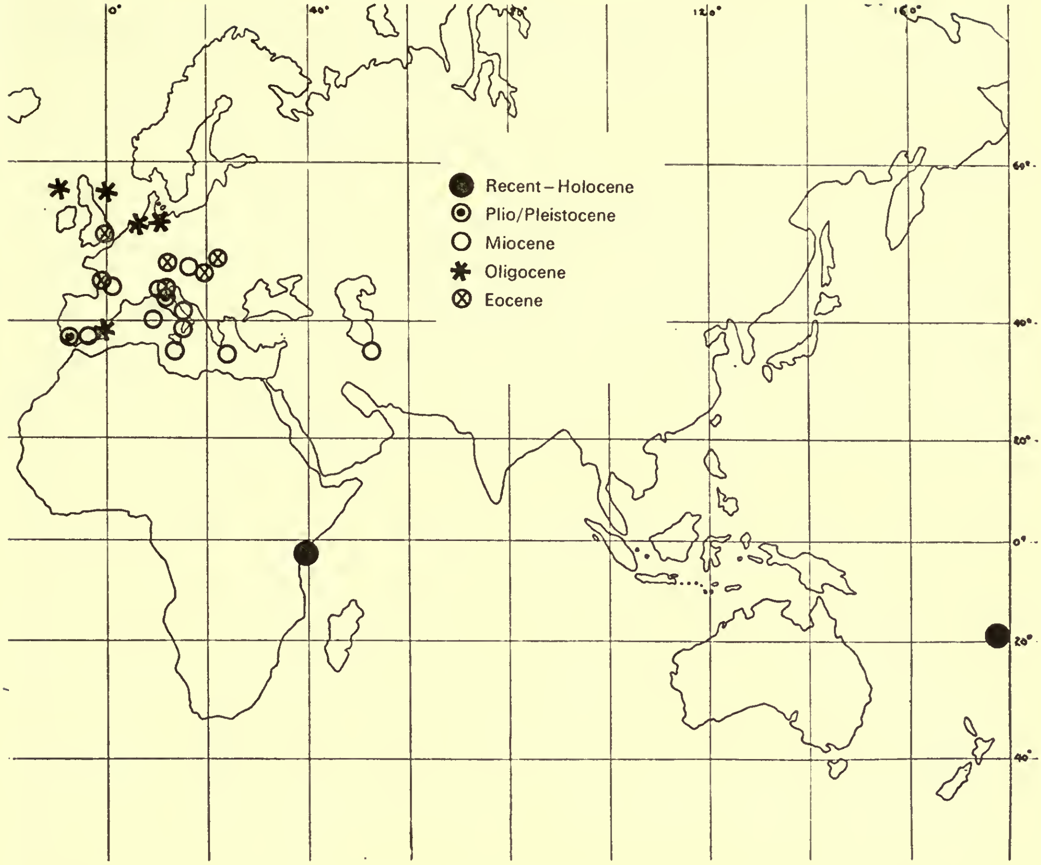
Appendix 1

The following records of *Batopora* have been plotted on Map 1. Many records include more than one species ; previously unpublished observations are noted thus '(R. L. obs.)'.

RECENT. Zanzibar, 805 m (Cook, 1966) : *B. murrayi.*
Fiji, Challenger Stn 174D, 384 m (P. L. C. obs.) : *B. murrayi.*

PLIOCENE. Sassuolo, near Modena, Italy (Namias, 1891) : *B. rosula.*
Huelva-1 well, near Huelva, Spain, 648 m (ditch cuttings) (R. L. obs.) : *B. rosula.*

MIOCENE. Crete, Sample 6–27, Almiri section (R. L. obs.) : *B. rosula.*
Malta, Sample PLR 4067, Blue Clay Formation (R. L. obs.) : *Batopora* sp.
Arzeboun II, Prov. du Mäzänderan, Iran (Dartevelle, 1948) : *B. ernii.*
Benestare, Calabria, Italy (Seguenza, 1880) : *B. rosula.*
N. Italy, Sample SM 55, Torre Veglio Section (R. L. obs.) : *Batopora* sp.
Abruzzi, Italy (Ceretti & Poluzzi, 1970) : *B. multiradiata.*
Sardinia, Sample MU 214, Gesturi-Furtei, Central N. Campidano (R. L. obs.) : *Batopora* sp.
Baden, near Vienna (Reuss, 1848) : *B. rosula.*
W. Aquitaine Basin (Le Saint, 1961) : *B. rosula* and *B. multiradiata.*
R.1103, Cuidad Granada Formation (*Globorotalia kugleri* zone), Velez Rubio, T. B. Roep Coll. (R. L. obs.) : *B. rosula.*


0°
40°
80°
120°
160°
60°
40°
20°
0°
20°
40°
● Recent – Holocene
⦿ Plio/Pleistocene
○ Miocene
✱ Oligocene
⊗ Eocene

MAP 1. Distribution of species of *Batopora* in time and space (see Appendix 1).

OLIGOCENE. Rockall Plateau, Site 117, 1038 m (Cheetham & Håkansson, 1972) : *Batopora* sp.

Boring K 62, 23.90–24, 80 m surface, Ijzendijke, Netherlands (presumably Boom Clay, Rupelian) (R. L. obs.) : *B. asterizans* sp. nov.

North Sea, Whitehall 43/3–1 well, 840–870 ft ditch cuttings (R. L. obs.) : *B. asterizans* sp. nov.

Spain, Samples K 48–50, Moli de Llinares, Villajoyosa, Alicante Province (R. L. obs.) : *B. multiradiata*.

Calbe and Saale, Germany (Reuss, 1867) : *B. stoliczkai*.

EOCENE. Skalnik, Central Carpathians (Malecki, 1963) : *B. multiradiata* and *B. stoliczkai*.

Buda, Marne de Buda (Couches à *Clavulinoides szaboi*) (Cook, 1966) : *B. multiradiata*.

Götzreuth, Bavaria (Koschinsky, 1885) : *B. scrobiculata* and *B. multiradiata*, and (P. L. C. obs.) USNM and BM : *B. grandis*.

Priabona and other northern Italian localities (Reuss, 1869; Waters, 1891; Braga, 1963): *B. multiradiata*, *B. stoliczkai* and *B. rosula*.

Bordeaux area (Labracherie, 1961): *B. stoliczkai*.

Sydenham and Hampstead, London Clay (Gregory, 1893): *B. clithridiata*.

Appendix 2

The following records of *Lacrimula* and *Atactoporidra* have been plotted on Map 2.

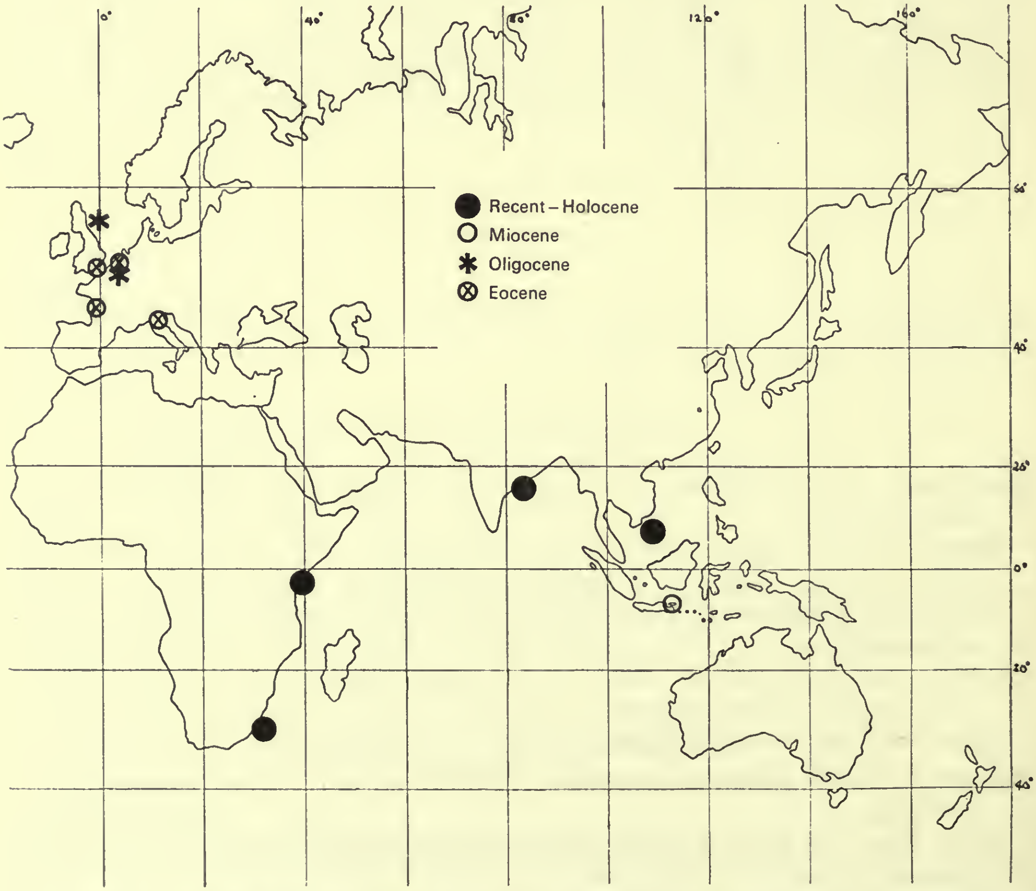
RECENT. Zanzibar, 101 and 207 m (Cook, 1966): *L. burrowsi*, and *L. pyriformis*.

S.E. Africa, near Durban, 102 m (Cook, 1966): *L. burrowsi*.

S. China Sea, 677 m (P. L. C. obs.): *Lacrimula* sp.

HOLOCENE. Bay of Bengal, E. India, 89 m (Rao & Rao, 1973): *L. visakhensis*.

MIOCENE. Sample BG 312, Kombangan, Madura, Indonesia (N.E. Java) (R. L. obs.): *L. similis* sp. nov., and *L. asymmetrica* sp. nov.



MAP 2. Distribution of species of *Lacrimula* and *Atactoporidra* in time and space (see Appendix 2).

Sample G 5671, west of Batuputih, Madura, Indonesia (R. L. obs.) : *L. grunaui* sp. nov.

OLIGOCENE. North Sea, Whitehall 43/3–1 well, 840–870 ft ditch cuttings (R. L. obs.) : *L. borealis* sp. nov.

Belgium, Tongrian, Rupelian (Canu & Bassler, 1931) : *Atactoporidra bredaniana.*

EOCENE. Near Verona, and near Possagno, N. Italy (Accordi, 1947, and P. L. C. obs.) : *L. perfecta.*

Belgium, Wemmelian (Canu & Bassler, 1931) : *A. bredaniana.*

Selsey, Barton Clay, England (Cheetham, 1966) : *A. glandiformis.*

Marcheprime, Gironde (Labracherie, 1961) : *A. globosa.*

Appendix 3

The following records of *Conescharellina* have been noted. Those marked with an asterisk (*) are plotted on Map 3.

RECENT

Japan	*41°36′N, 140°36′E, no depth	(Canu & Bassler, 1929)	*C. catella*
	41°31′N, 140°36′E, 80·5 m		*C. parviporosa*
	*35°N, 139°E, 300 m	(Silén, 1947)	*C. striata*
	35°N, 131°E	(Harmer, 1957)	*C. catella*
	33°N, 129°E, no depth	(Silén, 1947)	*Conescharellina* spp.
	*33°05′N, 130°03′E, 40 m	(Silén, 1947)	*C. striata*
Hong Kong	*21°33′N, 116°15′E, 161 m	(Canu & Bassler, 1929)	*C. concava*
Philippines	13°21′N, 122°18′E, 970 m	(Canu & Bassler, 1929)	*C. breviconica*
	12°15′N, 123°57′E, 146 m	(Canu & Bassler, 1929)	*C. breviconica*
			C. milleporacea
			C. catella
	12°04′N, 124°04′E, 193 m	(Canu & Bassler, 1929)	*C. breviconica*
	11°09′N, 123°50′E, 60·5 m	(Canu & Bassler, 1929)	*C. milleporacea*
			C. breviconica
	*10°01′N, 124°42′E, 216 m	(Canu & Bassler, 1929)	*C. breviconica*
Celebes Sea	*6°44′N, 121°E, 46 m	(Canu & Bassler, 1929)	*C. jucunda*
			C. delicatula
			C. obliqua
	6°11′N, 121°08′E, 295·5 m	(Canu & Bassler, 1929)	*C. jucunda*
			C. delicatula
	6°09′N, 120°58′E, 53 m	(Canu & Bassler, 1929)	*C. milleporacea*
			C. elongata
	6°05′N, 121°02′E, 35 m	(Canu & Bassler, 1929)	*C. catella*
			C. grandiporosa
			C. elongata
	6°04′N, 120°58′E, 37 m	(Canu & Bassler, 1929)	*C. milleporacea*
			C. elongata
	5°41′N, 120°27′E, 44 m	(Canu & Bassler, 1929)	*C. milleporacea*
	5°41′N, 120°47′E, 38 m	(Canu & Bassler, 1929)	*C. lunata*
			C. elongata
	5°30′N, 120°07′E, 612 m	(Canu & Bassler, 1929)	*C. radiata*
	5°24′N, 120°27′E, 44 m	(Canu & Bassler, 1929)	*C. elongata*

RECENT (*cont.*)

Celebes Sea (*cont.*)	5°20′N, 119°58′E, 440 m	(Canu & Bassler, 1929)	*C. milleporacea*
	5°10′N, 119°47′E, 421 m	(Canu & Bassler, 1929)	*C. elongata* *C. catella*
	4°54′N, 119°09′E, 310 m	(Canu & Bassler, 1929)	*C. radiata*
Malacca Str.	*4°20′N, 99°35′E, 50 m	(Silén, 1947)	*C. striata*
N. Celebes	1°N, 123°E, 72 m	(Harmer, 1957)	*C. elongata*
N. New Guinea	*0°, 130°E, 18–32 m	(Harmer, 1957)	*C. jucunda*
Makassar Straits & Java Sea	*1°19′S, 118°43′E, 2161 m	(Canu & Bassler, 1929)	*C. radiata* *C. transversa*
	2°S, 115°E, 59 m	(Harmer, 1957)	*C. catella*
	2°30′S, 107°10′E, 15–27 m	(Silén, 1947)	*C. brevirostris* *C. longirostris* *C. laevis*
off Java	*7°S, 115°E, 88 m	(Harmer, 1957)	*C. angustata*
	7°S, 115°E, 1060 m	(Harmer, 1957)	*C. distalis*
Java Sea	6°05′S, 114°07′E, 82 m	(Harmer, 1957)	*C. ovalis*
Arafura Sea	7°S, 132°E, 58·5–66 m	(BM)	*C. crassa*
Pt Moresby, Papua	*9°S, 147°E, no depth	(BM)	*C. crassa*
Torres Str.	9°, 140°E, 27·5–37 m	(BM)	*C. crassa*
Murray Is. Torres Str.	*10°S, 144°E, 27·5 m	(BM)	*C. conica*
Baudin Is. Timor Sea	12°S, 125′E, 27·5 m	(BM)	*Conescharellina* spp.
Holothuria Bank	*13°09′S, 126°22′E, 66–71 m	(BM)	*Conescharellina* spp.
	13°01′S, 125°58′E, 32 m	(BM)	*Conescharellina* spp.
E. Australia	14°S, 144°E, 24 m (P. Charlotte Bay)	(Waters, 1921)	*C. philippinensis*
	19°42′S, 148°21′E, 42 m (Holborn Is.)	(Waters, 1921)	*C. conica*
	27°30′S, 152°30′E, no depth	(Waters, 1921)	*C. philippinensis*
	*32°30′S, 152°30′E, 40–46 m (Pt Stephens)	(Waters, 1921)	*C. cancellata* *C. philippinensis* *C. angulopora*
	33°S, 152°E, no depth	(Waters, 1921)	*C. philippinensis*
	35 km E. of Pt Jackson, 146 m	(BM)	*C. biarmata* *C. angulopora* *C. eburnea*
S. E. Australia	36°S, 135°30′E, 190 m (56 km S.W. of Neptune Is.)	(BM)	*Conescharellina* sp.
	*40°S, 145°E, no depth (Bass Straits)	(Waters, 1921)	*C. angulopora*
S. E. Africa	*near Durban, 102 m	(Cook, 1966)	*C. africana*
E. Africa	*Zanzibar, 'Dalrymple' Stn 98, 69·5 m	(P. L. C. obs.)	*Conescharellina* sp.

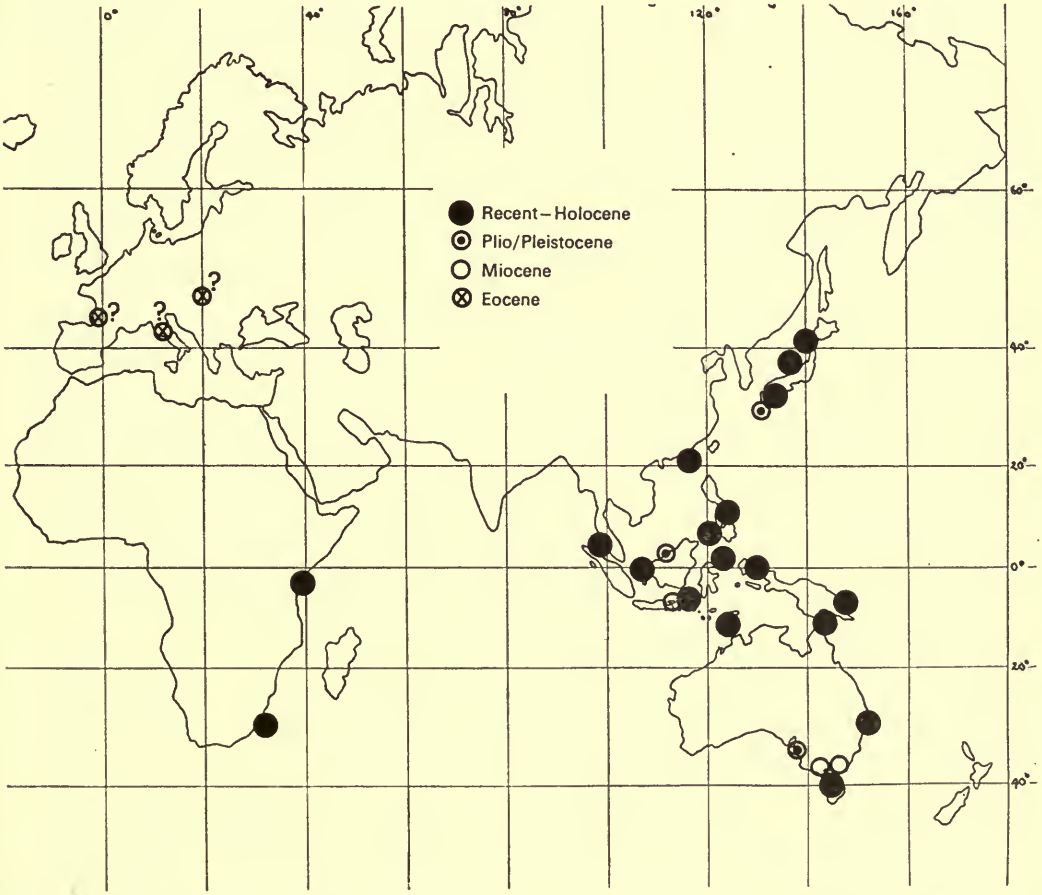
5/6

PLIOCENE-PLEISTOCENE

S. Japan	*28°N, 130°E (Kikai Jima)	(Kataoka, 1961)	*Conescharellina* sp.
Sarawak	*3°35′N, 112°55′E (Patricia Is.)	(R. L. obs.)	*Conescharellina* sp.
Australia	*Weymouth Bore, Adelaide, 310–330 ft	(BM, P. L. C. obs.)	*Conescharellina* sp.

MIOCENE

Australia	*Bairnsdale, Gippsland and Curdies Creek	(Waters, 1887–9)	*C. cancellata* *C. philippinensis*
Indonesia	*G 5671, W. of Batuputih, Madura	(P. L. C. obs.)	*Conescharellina* sp.


0°
40°
80°
120°
160°
60°
40°
20°
0°
20°
40°
● Recent–Holocene
⊙ Plio/Pleistocene
○ Miocene
⊗ Eocene
?
?
?

MAP 3. Distribution of species of *Conescharellina* and some problematical conescharelliniform species in time and space (see Appendix 3).

Eocene

Italy	*Mosciano, Italy	(Waters, 1921)	*C. eocoena* ?
Hungary	*Budapest	(Waters, 1921)	*C. eocoena* ?
France	*Landes, S. of Bordeaux	(Labracherie, 1970, 1971)	*Conescharellopsis vigneauxi* ?

REFERENCES

Accordi, B. 1947. Nuove forme di briozoi eocenici. *Studi trentini*, **25** : 103–110.

Annoscia, E. 1968. Briozoi. Introduzione allo studio con particolare riguardo ai briozoi italiani e mediterranei. *Palaeontogr. ital.* Pisa : 1–397.

Banta, W. C. 1972. The body wall in cheilostome Bryozoa. V. Frontal budding in *Schizoporella unicornis floridana*. *Mar. Biol. Berlin*, **14**, 1 : 63–71.

Bassler, R. C. 1935. Bryozoa (Generum et Genotyporum Index et Bibliographia). *In* W. Quenstedt, *Fossilium Catalogus* 1 : *Animalia*, pt 67 : 1–229.

—— 1953. Bryozoa. *In* R. C. Moore, *Treatise on invertebrate paleontology*, Pt G : G1–G253.

Boardman, R. S. & Cheetham, A. H. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa. *In* R. S. Boardman, A. H. Cheetham & W. A. Oliver, *Animal colonies*. Stroudsburg.

—— —— & Cook, P. L. 1969. Intracolony variation and the genus concept in Bryozoa. *Proc. N. Am. Paleont. Convent.* : 294–320.

Boekschoten, G. J. 1967. Eine Fauna aus dem Glaukonitsand van Ootmarsum (Miozön, Niederlande). *Natuurh. Maandbl.* **56e**, 3 : 39–48.

Braga, G. 1963. I briozoi del Terziario veneto. *Boll. Soc. paleont. ital.*, **2**, 1 : 16–55.

—— & Munari, M. 1972. Studi biometrici su due popolazioni di *Conescharellina* . . . dell'Eocene superiore del Veneto. *Studi trentini*, Sez. A, **49**, 2 : 111–126.

Canu, F. & Bassler, R. S. 1917 A synopsis of American Early Tertiary Cheilostome Bryozoa. *Bull. U.S. natn. Mus.* **96** : 1–87.

—— —— 1920. North American Early Tertiary Bryozoa. *Bull. U.S. natn. Mus.* **106** : 1–879.

—— —— 1923. North American Later Tertiary and Quaternary Bryozoa. *Bull. U.S. natn. Mus.* **125** : 1–302.

—— —— 1929a. Bryozoa of the Philippine Region. *Bull. U.S. natn. Mus.* **100**, 9 : 1–685.

—— —— 1929b. Bryozoaires éocènes de la Belgique. *Mém. Mus. r. Hist. nat. Belg.* **39** : 1–68.

—— —— 1931. Bryozoaires oligocènes de la Belgique. *Mém. Mus. r. Hist. nat. Belg.* **50** : 1–24.

Ceretti, E. & Poluzzi, A. 1970. Osservazioni su alcuni Briozoi Miocenici del Vallone di Santo Spirito in Abruzzo. *Annls Mus. geol. Bologna*, ser. 2a, **36** (1968) 2 : 743–750.

Cheetham, A. H. 1966. Cheilostomatous Polyzoa from the Upper Bracklesham Beds (Eocene) of Sussex. *Bull. Br. Mus. nat. Hist.* (Geol.), **13**(1) : 1–115.

—— 1968. Morphology and systematics of the bryozoan genus *Metrarabdotos*. *Smiths. misc. Collns.*, **153**, 1 : 1–121.

—— & Håkansson, E. 1972. Part 8. Sites 116 & 117. Bryozoa. *In* A. S. Laughton, W. A. Berggren *et al.*, *Initial reports of deep sea drilling project*, **12** : 395–671. Washington.

Cockbain, A. E. 1971. Tertiary Cheilostomatous Bryozoa from Victoria. *Proc. R. Soc. Vict.*, **84**, 1 : 173–182.

Cook, P. L. 1963. Observations on live lunulitiform zoaria of Polyzoa. *Cah. Biol. mar.* **4**, 4 : 407–413.

—— 1965. Polyzoa from West Africa, the Cupuladriidae. *Bull. Br. Mus. nat. Hist.* (Zool.), **13**, 6 : 189–227.

—— 1966. Some 'sand fauna' Polyzoa (Bryozoa) from eastern Africa and the northern Indian Ocean. *Cah. Biol. mar.* **7** : 207–223.

—— 1973. Settlement and early colony development in some Cheilostomata. *In* G. P. Larwood, *Living and fossil Bryozoa*. London & New York.

Cosijn, A. J. 1938. Statistical studies on the phylogeny of some Foraminifera . . . from the East Indies. *Leid. geol. Meded.*, **10** : 1–61.

Dartevelle, E. 1933. L'étude des Bryozoaires fossiles de l'Eocène de la Belgique. *Ann. soc. roy. Zool. Belge*, **63** : 55–116.

—— 1948. Note sur un Bryozoaire fossile de l'Iran. *Verh. naturf. Ges. Basel*, **59** : 75–79.

Eitan, G. 1972. Types of metamorphosis and early astogeny in *Hippopodina feegeensis* (Busk) (Bryozoa Ascophora). *J. exp. mar. Biol. Ecol.*, **8** : 27–30.

Gower, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **53** : 325–338.

Greeley, R. 1967. Natural orientation of lunulitiform bryozoans. *Bull. geol. Soc. Am.* **78** : 1179–1182.

Gregory, J. W. 1893. On the British Palaeogene Bryozoa. *Trans. zool. Soc. Lond.* **13**, 6 : 219–279.

Harmer, S. F. 1957. The Polyzoa of the Siboga Expedition. Pt IV, Cheilostomata Ascophora II . . . . *Rep. Siboga Exped.* **28d** : i–xv, 641–1147.

Hastings, A. B. 1964. The Cheilostomatous Polyzoa *Neoeuthyris woosteri* (MacGillivray) and *Reginella doliaris* (Maplestone). *Bull. Br. Mus. nat. Hist.* (Zool.), **11**, 3 : 245–262.

Haswell, W. A. 1880. On some Polyzoa from the Queensland coast. *Proc. Linn. Soc. N.S.W.* **5** : 33–44.

Héjjas, I. 1894. Adatok erdély Tertiär Bryozoa–Faunájához. (Beiträge zur kenntniss der Tertiare Bryozoenfauna Siebenburgens.) *Ert. erdel. Mus.-Egyes. Orvos. Term.-Tudom. Szakoszt.* **19**, 2, 16 : 113–152 ; **19**, 2, 17 : 201–216 ; **19**, 3, 16 : 217–260.

Hsu, K. J., Ryan, W. B. F. & Cita, M. B. 1972. Late Miocene desiccation of the Mediterranean. *Nature, Lond.* **242** : 240–244.

Jullien, J. 1883. Dragages du 'Travailleur'. Bryozoaires. Espèces draguées dans l'Océan atlantique en 1881. *Bull. Soc. zool. Fr.*, **7** : 497–529.

Kataoka, J. 1957. Bryozoa from the Daishaka Formation (Pliocene) . . .. *Trans. Proc. paleont. Soc. Japan*, n.s., **28** : 143–153.

—— 1961. Bryozoan fauna from the 'Ryukyu Limestone' of Kikai-jima, Kagoshima Prefecture, Japan. *Sci. Rep. Tohoku Univ. Geol.* **32**, 2 : 213–272.

Koschinsky, C. 1885. Bryozoen Fauna der älteren Tertiärschichten des südlichen Bayerns. I, Cheilostomata. *Palaeontographica*, **32** : 1–73.

Labracherie, M. 1961. Les Bryozoaires éocènes du sous-sol du Bordelais. Observations paléontologiques et biostratigraphiques. Thèse, 3me Cycle d'Enseignement supérieur, pp. 1–210. Laboratoire de Géologie approfondie, Université de Bordeaux.

—— 1970. Les Bryozoaires dans l'Eocène Nord-Aquitain. Signification biostratigraphique et paléoécologique, **1** : 1–141, i–xxxiv ; **2** : 142–314 ; **3**, tables 1–36. Thèse de doctorat d'état des Sciences naturelles . . . de l'Université de Bordeaux No. 316.

—— 1971. Evolution générale des assemblages de Bryozoaires dans l'Eocène du bassin nord-aquitain. *Somm. Séa. Soc. géol.* **21** : 388–389.

Lagaaij, R. 1963a. *Cupuladria canariensis* (Busk)–portrait of a bryozoan. *Palaeont.* **6**, 1 : 172–217.

—— 1963b. New Additions to the Bryozoan fauna of the Gulf of Mexico. *Publ. Inst. mar. Sci. Univ. Texas*, **9** : 162–236.

Le Saint, A. 1961. Etude paléontologique et biostratigraphique des Bryozoaires girondiens du Bassin ouest-Aquitain. Thèse, 3me Cycle d'Enseignement supérieur. No. 123 : 1–223. Laboratoire de Géologie approfondie, Université de Bordeaux.

MacGillivray, H. J. 1971. Variability of Foraminifera. Pt II, Standard level of variability. *Proc. K. med. Akad. Wet.* ser. B, **74**, 2 : 206–238.

Malecki, J. 1952. Les Bryozoaires des sables à Hétérostégines aux environs de Cracovie et Miéchow. *Ann. Soc. géol. Pologne*, **21**, 2 : 181–234.

—— 1963. [Bryozoa from the Eocene of the Central Carpathians between Grybów and Dukla]. *Pr. geol.* **16** : 7–158 (in Polish).

MAPLESTONE, C. M. 1904. Tabulated list of the fossil Cheilostomatous Polyzoa in the Victorian Tertiary deposits. *Proc. r. Soc. Vict.* **17**, 1 : 182–219.

—— 1910. Observations on *Parmularia obliqua* and a fossil species. *Proc. r. Soc. Vict.* **23**, 1 : 42–43.

NAMIAS, I. 1891. Contributo ai Briozoi Pliocenici delle provincie di Modena e Piacenza. *Boll. Soc. geol. Ital.* **9** : 471–513.

NEVIANI, A. 1895. Briozoi Eocenici de calcare nummulitico. *Boll. Soc. geol. Ital.* **14**, 2 : 119–127.

OSSAT, ANGELIS G. DE & NEVIANI, A. 1897. Corallarii e Briozoi Neogenici di Sardegna. *Boll. Soc. geol. Ital.* **15**, 4 : 571–595.

RAO, M. S. & RAO, T. K. 1973. A new bryozoan species from the shelf sediments off the East Coast of India. *Curr. Sci.* **42**, 14 : 506–507.

REUSS, A. E. 1848. Die fossilen Polyparien des Wiener Tertiärbeckens. *Haidingers Naturhistorisches Abhandl.* II. Vienna.

—— 1867. Über einige Bryozoen aus dem deutschen Unterologocän. *Sber. Akad. Wiss. Wien,* **55**, 1 : 216–234.

—— 1869. Paläontologische Studien über die älteren Tertiärschichten der Alpen. II. Die fossilen Anthozoen und Bryozoen der Schichtengruppe von Crosara. *Sber. Akad. Wiss. Wien,* **58** : 288–292.

SEGUENZA, G. 1880. Le formazioni Terziare nella provincia di Reggio (Calabria). *Atti Acad. Lincei,* ser. 3, **6** : 1–446.

SILÉN, L. 1947. Conescharellinidae (Bryozoa Gymnolaemata) collected by Prof Dr Sixten Bock's Expedition to Japan and the Bonin Islands, 1914. *Ark. Zool.* **39A**, 9 : 1–61.

SISSINGH, W. 1972. Late Cenozoic Ostracoda of the South Aegean Island arc. *Utrecht Micropal. Bull.* **6** : 1–187.

SOLDANI, A. 1780. Saggio orittografico ovvero osservazioni sopra le terre nautiliche ed ammonitiche della Toscana. Sienna.

VAN DER VLERK, I. M. & POSTUMA, J. A. 1967. Oligo-Miocene *Lepidocyclinas* and planktonic Foraminifera from East Java and Madura, Indonesia. *Proc. K. ned. Akad. Wet.* ser. B, **70**, 4 : 391–398.

WATERS, A. W. 1891. North-Italian Bryozoa. Pt 1, Cheilostomata. *Q. Jl. geol. Soc.* **47** : 1–34.

—— 1919. *Batopora* and its allies. *Ann. Mag. nat. Hist.* (9), **3** : 79–94.

—— 1921. Observations on the relationships of the Selenariidae. *J. Linn. Soc. Zool.* **34** : 399–427.

P. L. COOK
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

PLATE 1

Batopora and *Trochosodon* – early astogenetic stages.
Photographs by scanning electron microscope.

Fig. 1. *B. stoliczkai* Reuss. NMV 1867.XII, 13a–d, Bünde, Germany, Oligocene. Diameter of colony 0·72 mm. × 71.

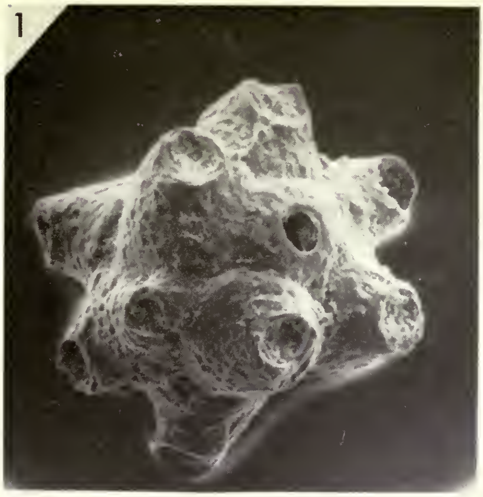
Fig. 2. *B. murrayi* Cook. BM 'Dalrymple' Stn 98, Zanzibar, Recent. Diameter of colony 0·63 mm. × 95.

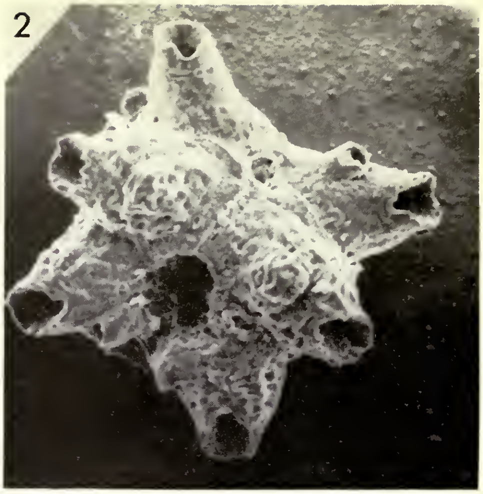
Fig. 3. *Trochosodon* sp. 1. BM 'Challenger' Stn 185, off Cape York, N. Australia, Recent. Diameter of colony 0·93 mm. × 71.

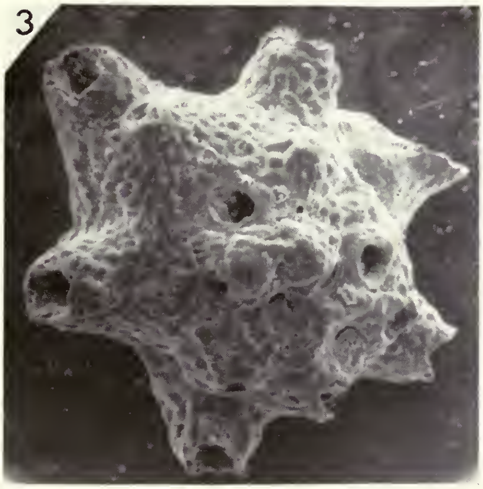
Fig. 4. *Trochosodon* sp. 1. BM as above, showing specialized rootlet pores (lunoecia, arrowed). × 178.

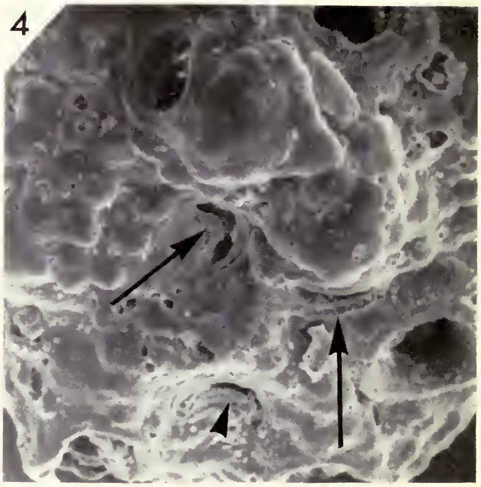
Fig. 5. *Trochosodon* sp. 2. BM as above, very young colony with ovicell and lunoecia (arrowed). Diameter of colony 0·84 mm. × 85.

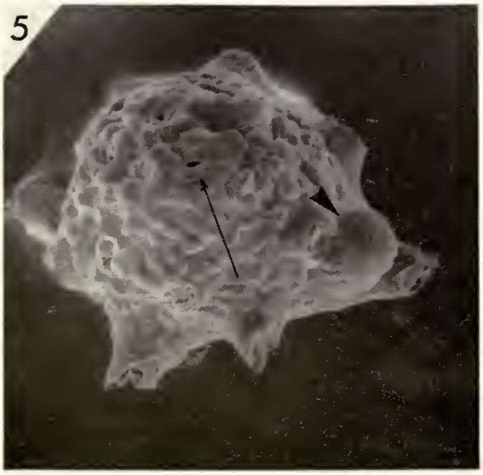
Fig. 6. *Trochosodon* sp. 2. BM as above, lateral view of colony ; note extensive development of apical tissues. × 85.

1


2


3


4


5


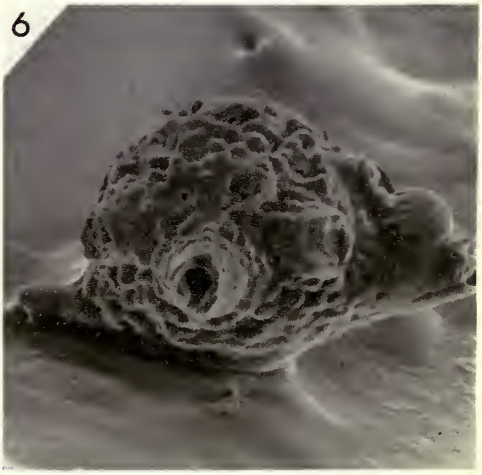
6


PLATE 2

Batopora. Photographs by scanning electron microscope.

FIG. 1. *B. clithridiata* (Gregory). BM B1357, Sydenham, London Clay, Eocene. See also Pl. 5, fig. 5. × 45.

FIG. 2. *B. stoliczkai* Reuss. USNM, Calbe, Germany, Oligocene. Lateral view, note ovicells. × 73.

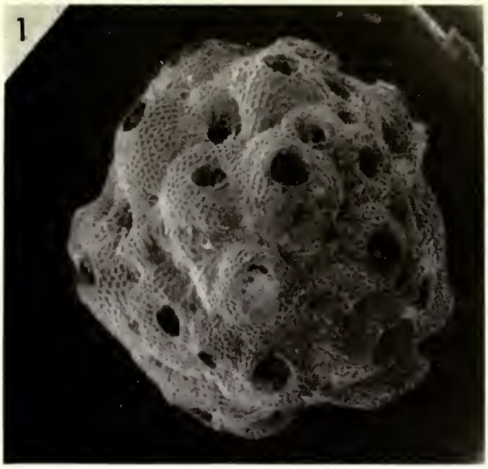
FIG. 3. *B. asterizans* sp. nov. North Sea, Middle Oligocene. Lateral-frontal view. × 72.

FIG. 4. *B. asterizans* sp. nov. As above, view of apical region. × 128.

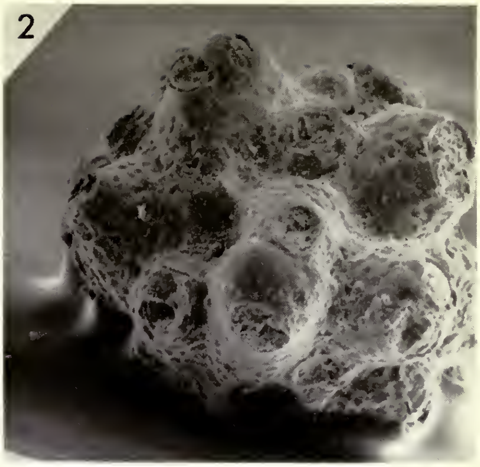
FIG. 5. *B. grandis* sp. nov. USNM 88882 pt., Götzreuth, Bavaria, Eocene. × 12.

FIG. 6. *B. grandis* sp. nov. As above, zooids with sinuate orifices and a broken ovicell. × 72.

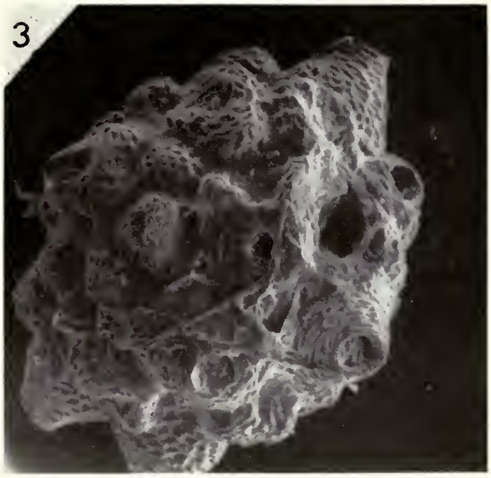
1



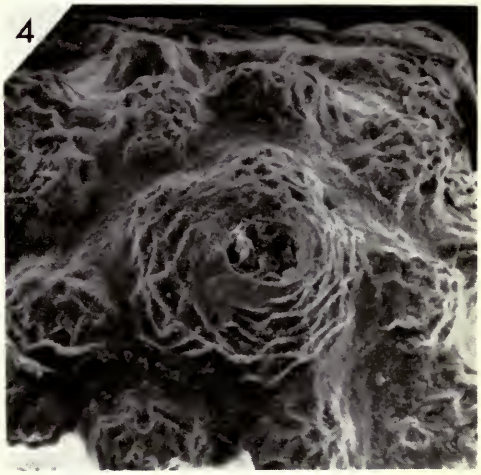
2



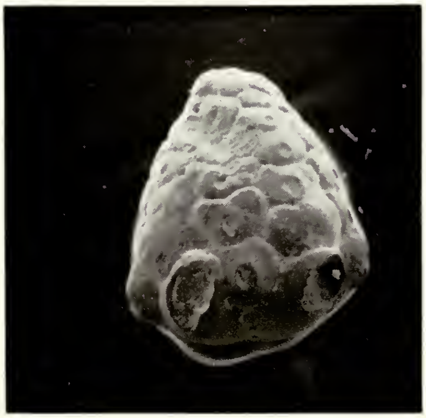
3



4



5



6

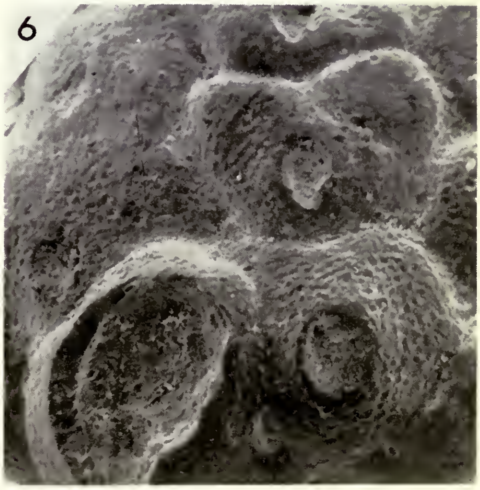


PLATE 3

Batopora.

FIG. 1. *B. multiradiata* Reuss. USNM 88881 pt., Götzreuth, Bavaria, Eocene. Young colony with one zone of change. × 21.

FIG. 2. *B. rosula* (Reuss). NMV Baden, Austria, Miocene. × 36.

FIG. 3. *B. rosula* (Reuss). NMV Baden, Austria, Miocene. × 36.

FIG. 4. *B. stoliczkai* Reuss. NMV, Bünde, Germany, Oligocene. × 36.

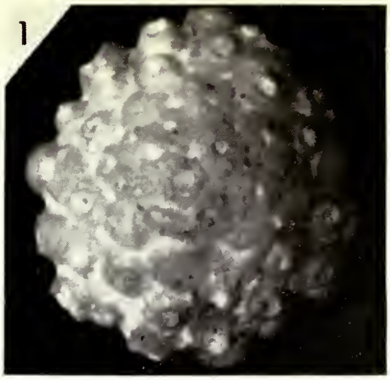
FIG. 5. *B. scrobiculata.* Koschinsky. USNM 88882 pt., Götzreuth, Bavaria, Eocene. Note ovicells. × 21.

FIG. 6. *B. scrobiculata.* Same specimen, antapical side of colony. × 21.

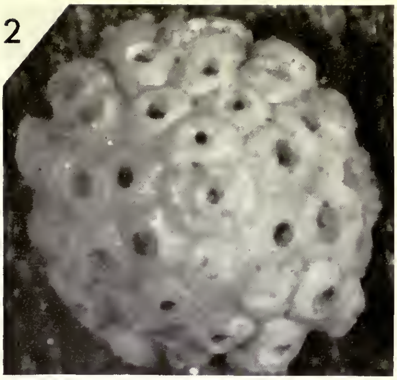
FIG. 7. *B. scrobiculata.* Same specimen, showing antapical axial kenozooids. × 21.

FIG. 8. *B. grandis* sp. nov. USNM 88882 pt., Götzreuth, Bavaria, Eocene. × 16.

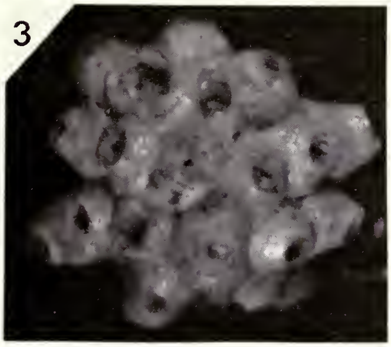
1



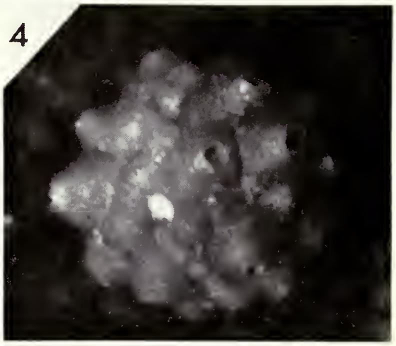
2



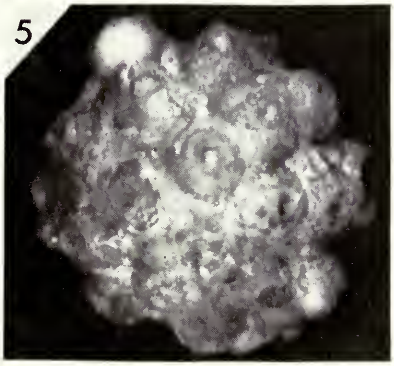
3



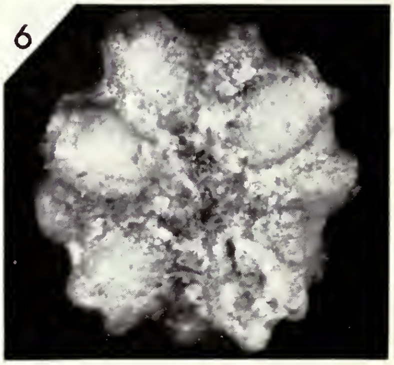
4



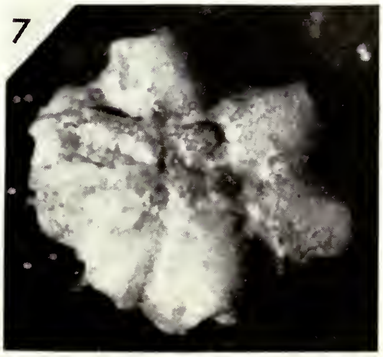
5



6



7



8

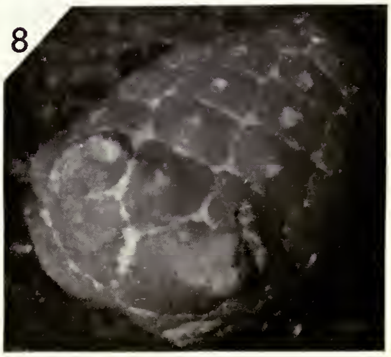


PLATE 4

Batopora and *Lacrimula*.

Photographs by scanning electron microscope (except Fig. 5).

FIG. 1. *B. rosula* (Reuss). Crete, Miocene. Lateral view, showing prominent secondarily budded apical kenozooid. × 44.

FIG. 2. *B. rosula*, as above, view from apical side. × 44.

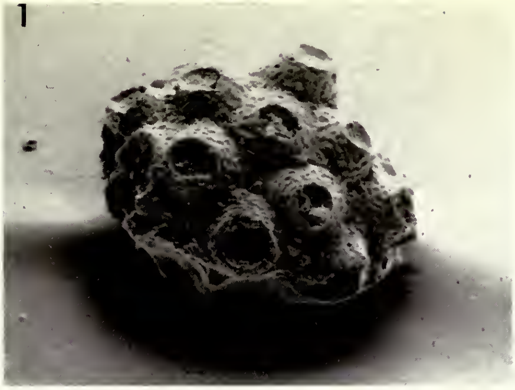
FIG. 3. *L. perfecta* (Accordi). BM, Possagno, N. Italy, Eocene. Proliferal region zooids showing orifice with lateral condyles (arrowed) and marginal pores. See also Pl. 7, fig. 1. × 105.

FIG. 4. *B. multiradiata* Reuss. USNM 88881 pt., Götzreuth, Bavaria, Eocene. Lateral view showing overgrowth of secondary zone zooids and broken ovicells (arrowed). × 28.

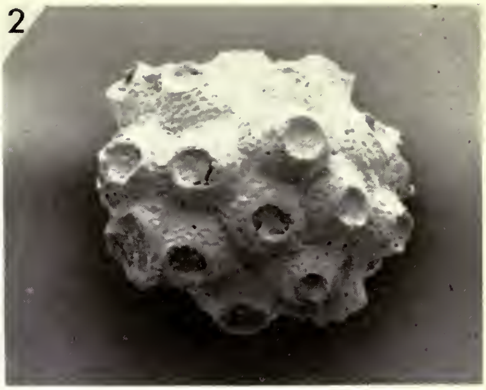
FIG. 5. *B. multiradiata*. USNM 71205, Val di Lonte, N. Italy, Bartonian, Eocene. Basal view. × 21.

FIG. 6. *B. multiradiata*, as above. Lateral view showing ovicells and tertiary series of apical zooids and kenozooids. × 25.

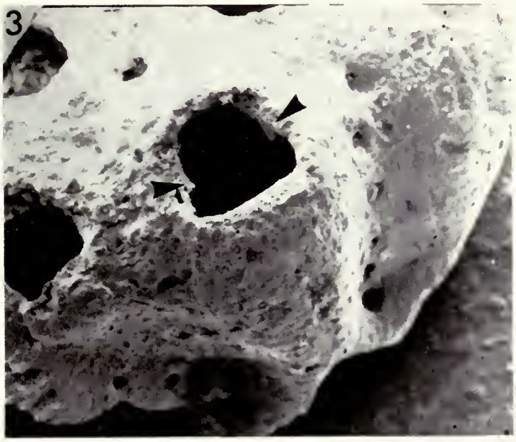
1



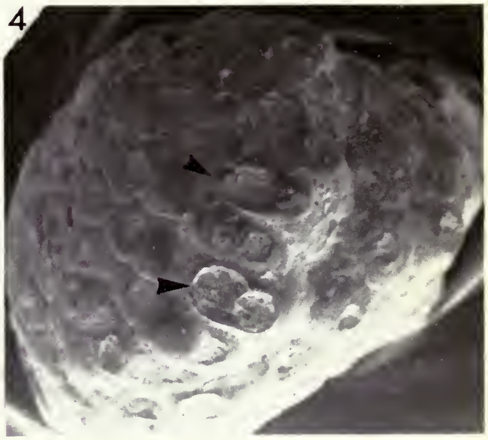
2



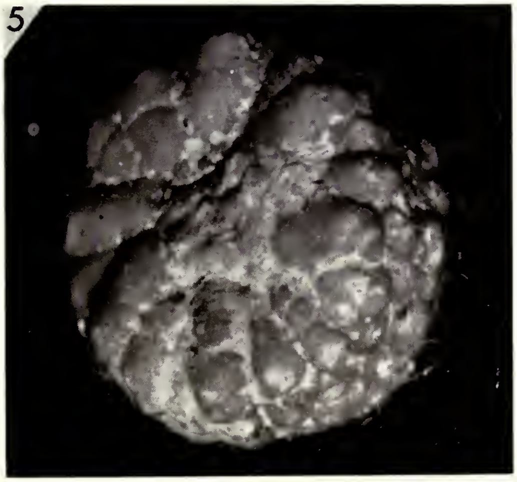
3



4



5



6

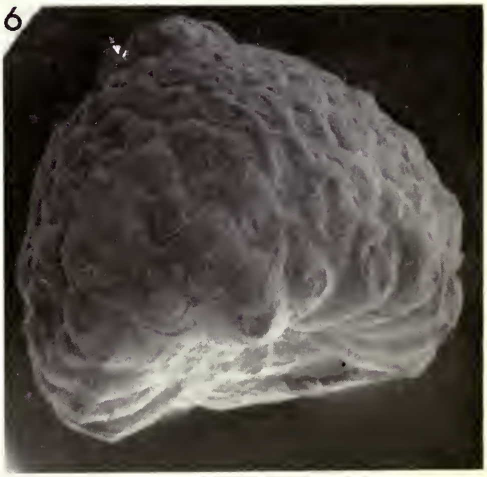


PLATE 5

Lacrimula, *Atactoporidra* and *Batopora*.
Photographs by scanning electron microscope.

FIG. 1. *L. burrowsi* Cook. BM 1965.8.24.9, Zanzibar, Recent. Apical region; note kenozooidal tube and secondarily budded zooids and avicularia. See also Pl. 6, fig. 3. × 81.

FIG. 2. *A. bredaniana* (Morren). BM D7864, Belgium, Eocene. Apical region; note similarity with *L. burrowsi*. See also Pl. 6, fig. 6. × 58.

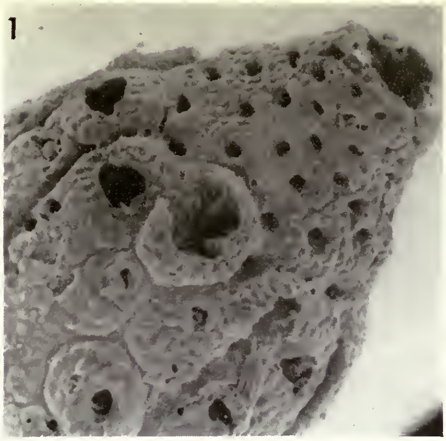
FIG. 3. *L. pyriformis* Cook. BM 1965.8.24.12, Zanzibar, Recent. Apical region; note the reticulation of the surface of the tube, and the regularly placed pores. See also Pl. 6, fig. 5. × 156.

FIG. 4. *L. asymmetrica* sp. nov. BG 312, W. Madura, Indonesia, Miocene. Apical region showing one of the pores. See also Pl. 7, fig. 3. × 104.

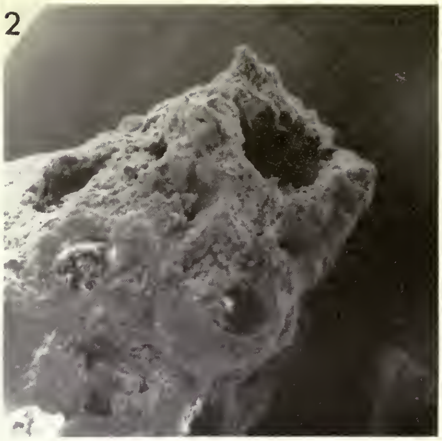
FIG. 5. *B. clithridiata* (Gregory). BM B1357, Sydenham, London Clay, Eocene. Interzooidal avicularium with complete bar (*av*). See also Pl. 2, fig. 1. 1. × 126.

FIG. 6. *L. burrowsi* Cook. BM 1965.8.24.9, Zanzibar, Recent. Ovicells and avicularia. × 74.

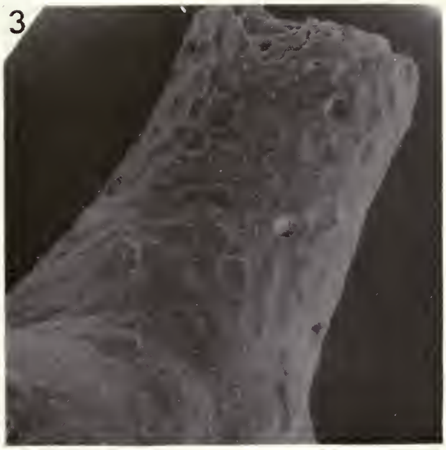
1



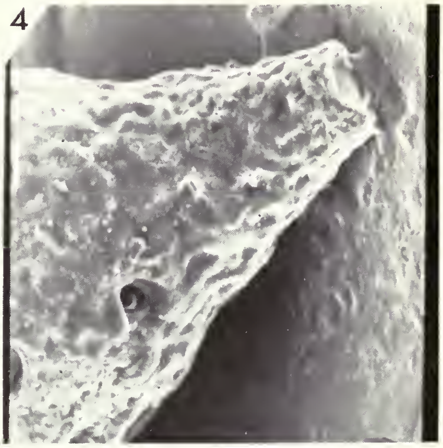
2



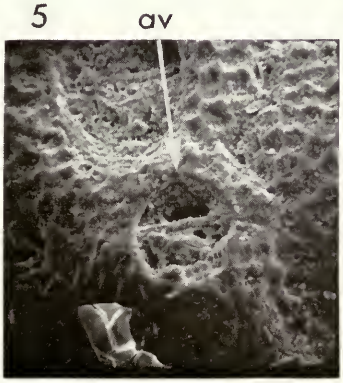
3



4



5



6

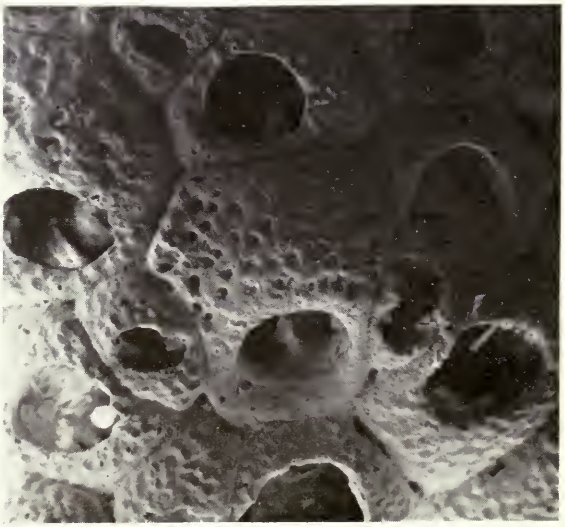


PLATE 6

Lacrimula and *Atactoporidra*. Photographs by scanning electron microscope.

Fig. 1. *L. similis* sp. nov. BG 312, Madura, Indonesia, Miocene. Colony with a secondary zone of change. × 57.

Fig. 2. *L. similis* sp. nov. As above, showing primary and secondary zone zooids with avicularia. × 57.

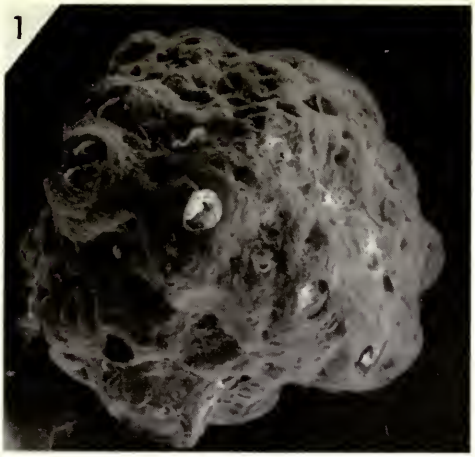
Fig. 3. *L. burrowsi* Cook. BM 1965.8.24.9, Zanzibar, Recent. View from the apical end of a colony. See also Pl. 5, fig. 1. × 34.

Fig. 4. *L. visakhensis* Rao & Rao. BM 1070.8.8.1, Bay of Bengal, India, Holocene. Colony with apical ovicells. × 38.

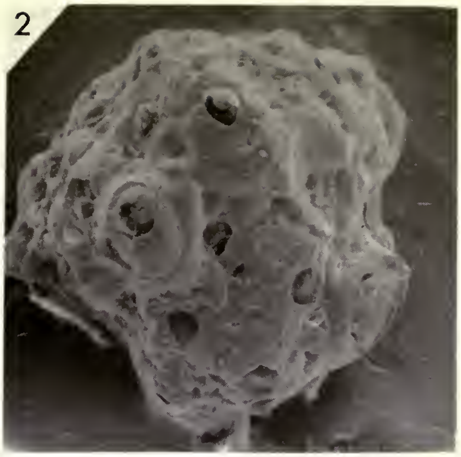
Fig. 5. *L. pyriformis* Cook. BM 1965.8.24.12, Zanzibar, Recent. Colony with ovicelled zooids in the proliferal whorl. See also Pl. 5, fig. 3. × 23.

Fig. 6. *A. bredaniana* (Morren). BM D7864, Belgium, Eocene. See also Pl. 5, fig. 2. × 30.

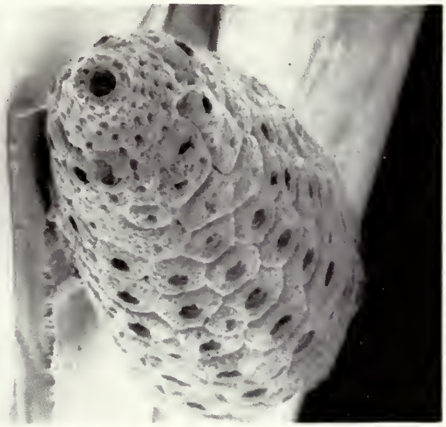
1



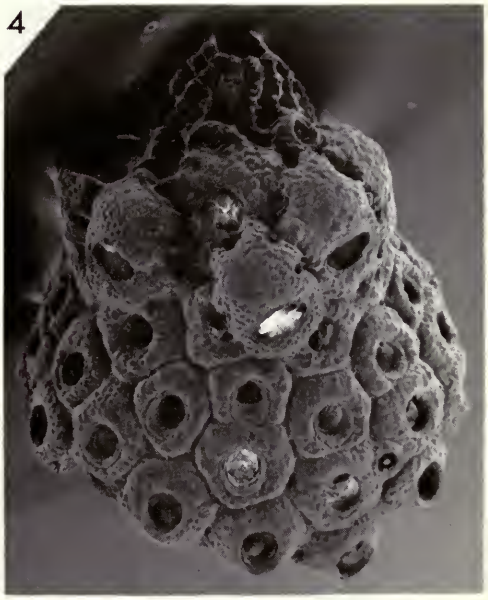
2



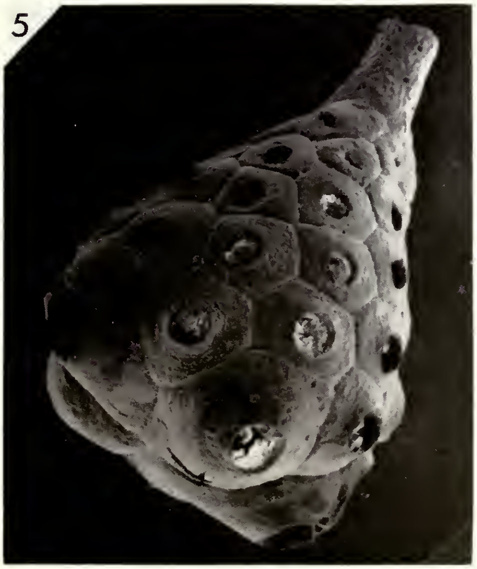
3



4



5



6

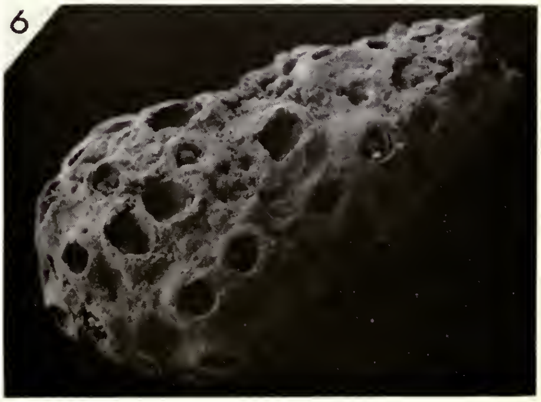


PLATE 7

Lacrimula. Photographs for Figs. 1–3 by scanning electron microscope.

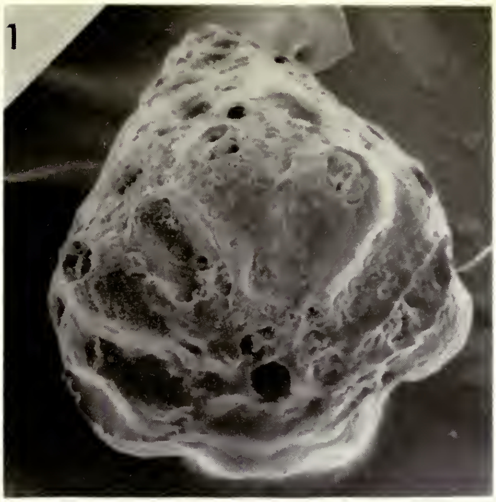
FIG. 1. *L. perfecta* (Accordi). BM, Possagno, N. Italy, Eocene. View of proliferal region, note axial kenozooids. See also Pl. 4, fig. 3. × 44.

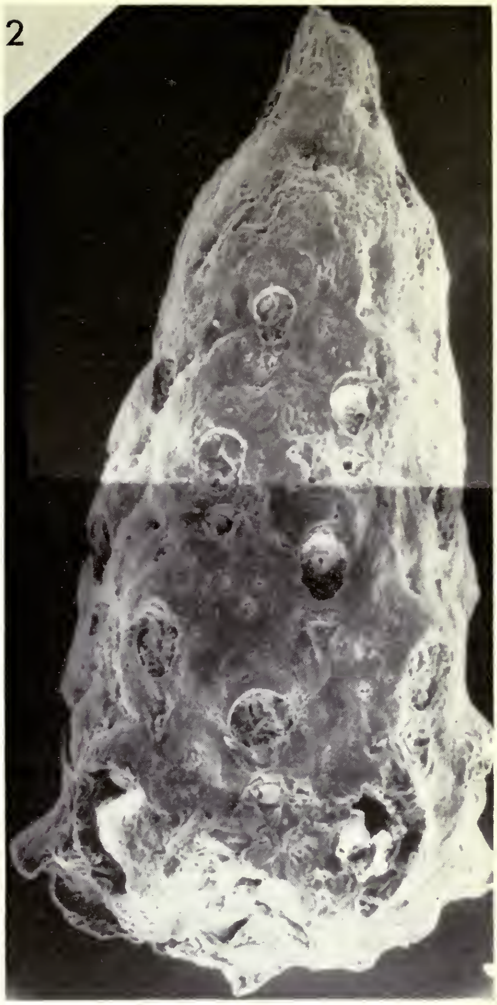
FIG. 2. *L. grunaui* sp. nov. G 5671, Madura, Indonesia, Miocene. × 81.

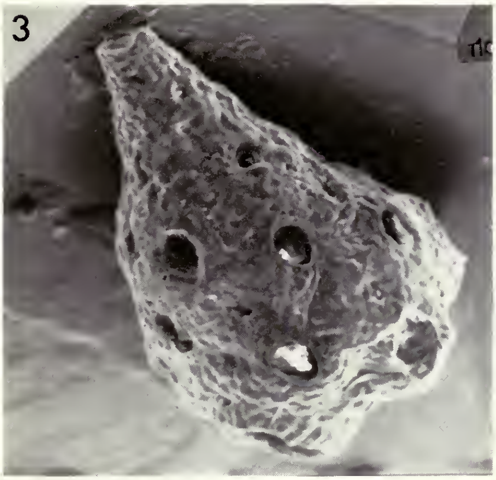
FIG. 3. *L. asymmetrica* sp. nov. BG 312, Madura, Indonesia, Miocene. See also Pl. 5, fig. 4. × 60.

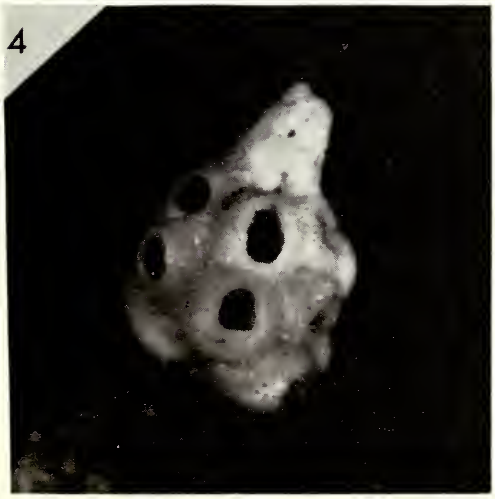
FIG. 4. *L. borealis* sp. nov. 43/3–1, North Sea, Oligocene. × 37.

FIG. 5. *L. borealis.* Same specimen. × 37.

1


2


3


4


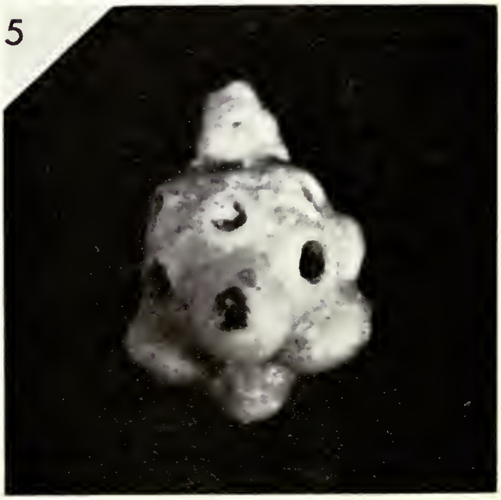
5


PLATE 8

Lacrimula burrowsi Cook – sections through restored colonies.

Fig. 1. Transverse section showing alternating zooid whorls. The zooids nearer the axis belong to the whorl adapical in position to the zooids at the periphery. Note the axial concentration of communicating tubules derived from marginal pores. Opercula and avicularian chambers arrowed. × 41.

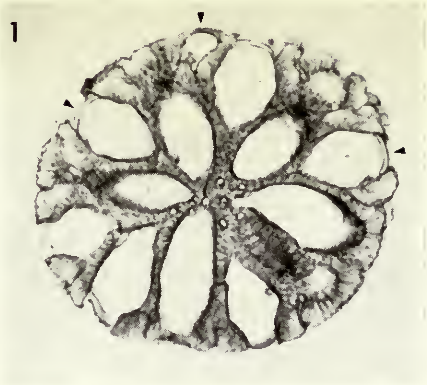
Fig. 2. Transverse section near antapical end of a large colony. Ovicells (large cavities) and avicularian chambers (small cavities) arrowed. × 28.

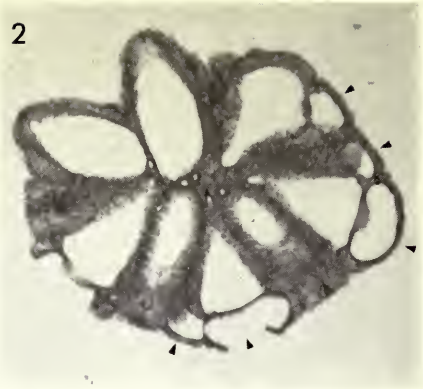
Fig. 3. Tangential longitudinal section through zooid orifices. Note the increase in size with astogenetic position. Marginal pores and condyles arrowed. × 41.

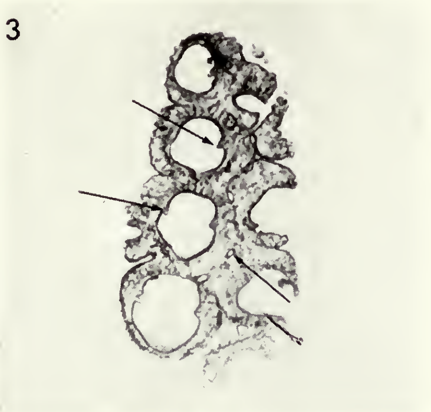
Fig. 4. Thick transverse section through an apical tube. Note passage of tubular kenozooidal cavities at an angle through the calcification from exterior to interior (arrowed). × 91.

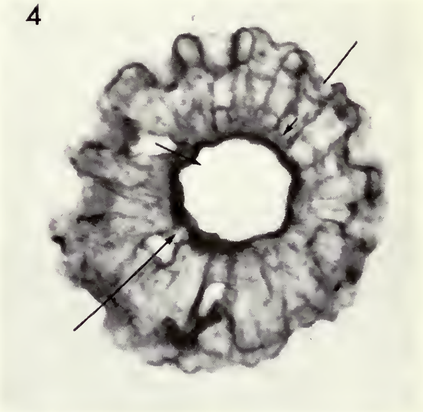
Fig. 5. Deep tangential longitudinal section of the apical region. Note tubular kenozooidal cavities passing through the calcification at various angles and tubules from pores connecting avicularian chambers with primary zooids. Avicularian chambers arrowed, *a*, a^1 zooids of ancestrular whorl. × 86.

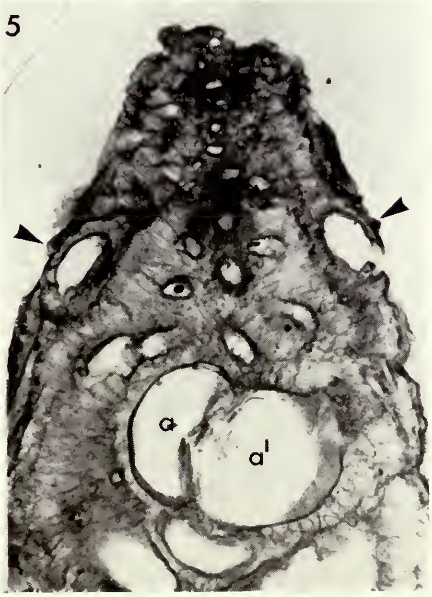
Fig. 6. Thick section through apical region of an astogenetically older colony. Note kenozooidal cavities and axial tube cavity with stained tissue. Kenozooidal cavities arrowed. × 91.

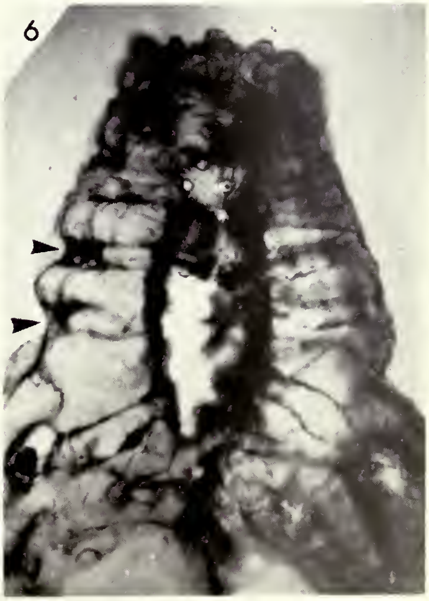

1


2


3


4


5


6

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. Kay, E. Alison. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.)
2. Whitehead, P. J. P. The Clupeoid Fishes described by Lacepède, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. Taylor, J. D., Kennedy, W. J. & Hall, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4·50.
4. Haynes, J. R. Cardigan Bay Recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. Pp. 245; 33 Plates, 47 Text-figures. 1973. £10·80.
5. Whitehead, P. J. P. The Clupeoid Fishes of the Guianas. Pp. 227; 72 Text-figures. 1973. £9·70.
6. Greenwood, P. H. The Cichlid Fishes of Lake Victoria, East Africa: the Biology and Evolution of a Species Flock. Pp. 134; 1 Plate, 77 Text-figures. 1974. £3·75. Hardback edition £6.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU